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Laterality in pigs and its links with personality, emotions and animal welfare

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DVM, MSc Charlotte Goursot
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Gutachter:

Prof. Dr. Birger Puppe

- Universität Rostock, Agrar- und Umweltwissenschaftliche Fakultät, Professur für Verhaltenskunde
- Leibniz-Institut für Nutztierbiologie (FBN) Dummerstorf, Institut für Verhaltensphysiologie, Abteilung Nutztierethologie

Prof. Dr. Beat Wechsler
Forschungsanstalt Agroscope Reckenholz-Tänikon ART, Tiergerechte Haltung

PD Dr. Lorenz Gygax
Humboldt-Universität zu Berlin, Lebenswissenschaftliche Fakultät, Albrecht Daniel Thaer-Institut für Agrar- und Gartenbauwissenschaften (Thaer-Institut), Tierhaltungssysteme

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List of Abbreviations

A	*Ambilateral, without any significant bias*
ANOVA	*Analysis of variance*
ANS	*Autonomic nervous systems*
BAS	*Behavioural activation system*
BIN	*Binocular*
BIS	*Behavioural inhibition system*
BT	*Backtest*
C	*Cortisol*
CCC	*Cubic clustering criterion*
CNS	*Central nervous system*
CV	*Coefficient of variation*
DurMax	*Duration of a vocalization from start to maximum amplitude*
EEG	*Electroencephalography*
F1	*Frequency of the first peak of a vocalization*
F2	*Frequency of the second peak of a vocalization*
FFFS	*Flight-fight-freeze system*
FFT	*Fast Fourier transform*
(f)MRI	*(functional) Magnetic resonance imaging*
fNIRS	*Functional near-infrared spectroscopy*
GFP	*General factor of personality*

HAT	*Human approach test*
HF	*High frequency*
HNR	*Harmonic-to-noise ratio of a vocalization*
HPA (axis)	*Hypothalamic pituitary adrenal (axis)*
HRV	*Heart rate variability*
L	*Left*
LAT	*Lateralized*
LEC	*Left eye covered*
LF	*Low frequency*
LI	*Laterality index*
LI_ABS	*Absolute value of the laterality index*
NOT	*Novel object test*
ODT	*Open door test*
OFT	*Open-Field test*
PNS	*Peripheral nervous system*
Q25	*First quartile of energy over the frequency range of a vocalization*
Q50	*Second quartile of energy over the frequency range of a vocalization*
Q75	*Third quartile of energy over the frequency range of a vocalization*
R	*Right*
REC	*Right eye covered*
RMSSD	*Root mean square of successive differences between interbeat intervals*
R-R (interval)	*Time between two consecutive R-peaks in an ECG*
RST	*Reinforcement sensitivity theory*
SDNN	*Standard deviation of all interbeat intervals of a data set*
SE	*Standard error*
SNS	*Somatic nervous system*
T	*Testosterone*
TMS	*Transcranial magnetic stimulation*

Preface

From mind-body dualism to affective states

Whether mind and body are two independent entities is one of the oldest philosophical questions which emerged from Plato's notion on dualism in his work *Phaedo* (Carone, 2005). This problem even exists from a linguistic point of view: the Latin word "*animus*"–which refers to the "rational soul of man"– shares the same origin with the word "*anima*"–which denotes the principle of animal life or anything that breathes (Lewis & Short, 1879, p. II.C.1.). Many philosophers consider that the contribution of Descartes (1637) to the mind-body dualism debate has played a decisive role in the evolution of modern Western culture (Müller & Krause, 1976) particularly during our industrial revolutions (Board, 2002; Duncan, 2006; Le Neindre et al., 2017). Nowadays, Cartesianism still influences our society from medicine to ecology (Gold, 1985; Leder, 1992; Preston, 2010).

The famous statement of Descartes "I think therefore I am" ("*Cogito ergo sum*") implies that the intelligent (human) mind is superior to any other living organisms ("automata") because *they do not think*. This interpretation represents the roots of anthropocentrism, defined as the overemphasis on the centrality of human values and concerns at the expense of non-human ones (Preston, 2010). As a result, it took a long time to foster the idea that the human brain works in a similar way as other mammalian brains. While Darwin (1859) significantly helped to deconstruct evolutionary anthropocentrism (i.e. humans are the most elaborate product of evolution), studies on comparative anatomy and psychology helped to deconstruct the belief that the human brain is evolutionary exceptional (Herculano-Houzel, 2011, 2019; Mota et al., 2019) or that some brain functions are "unique to human". Relevant examples are that non-human animals also experience mental states (Griffin, 1976; Staddon, 1989) with different levels of consciousness (Le Neindre et al., 2017; Wechsler, 2019); that a laminated cortex is not necessary for having elaborated cognitive skills (i.e. in birds Güntürkün, 2012); or that hemispheric specializations are present in all vertebrate taxa (Rogers et al., 2013, a central topic in this thesis). Nowadays, it is believed that convergent evolution (i.e. without a common ancestor) may explain the continuity of brain functions between many vertebrate taxa (Emery & Clayton, 2004; Güntürkün, 2012; Rattenborg et al., 2009).

Another consequence of the Cartesian dualism is that psychology and physiology were studied separately for a long time. Therefore, neurobiologists did not consider the study of "feelings" or affective states –another central topic of this thesis– as a scientific field for decades (Damasio, 1995; Lazarus, 1993), despite early descriptions of human emotions (Darwin, 1873; James,

1884; Wundt, 1897). Times changed when Freud argued for the existence of an unconscious mind which influences our rationality and our psychopathology (Freud, 1904; Grey, 1993). Later, Damasio (1994) even claimed the opposite of Descartes: "I am therefore I think", acknowledging the role of affective states as necessary to understand brain function (Dalgleish, 2004; LeDoux, 2000; Panksepp, 1998). Nowadays, the study of affective states in non-human animals is considered a promising means for understanding how behaviour is computed by the brain, and as such has implications for animal welfare (Gygax, 2017). This thesis will show that studying the links between hemispheric specializations and affective states in pigs contribute to perceiving these farm animals as individuals with complex brains. As a consequence, this may generate more empathy and understanding for those animals and could increase the public demand to improve their welfare.

"Dem Menschen, der zur Ethik der Ehrfurcht vor dem Leben gelangt ist, ist jedes Leben als solches heilig. Er hat Scheu davor, ein Insekt zu töten, eine Blume abzureißen. Den Wurm, der auf der Straße verschmachtet, errettet er, indem er ihn ins Gras legt."

Albert Schweitzer (1875-1965)

1 General Introduction

1.1 A brief history of animal welfare research and why animal brains matter

1.1.1 The emergence of the animal welfare concept

As a direct consequence of our industrial revolutions, the rise of animal production has been prioritized over the acknowledgment of animal sentience during the last two centuries (Porcher, 2014). Indeed, the pioneers of industrialisation of animal husbandry (e.g., Sanson, 1907) asserted farm animals were machines because it could justify their exploitation for the large-scale production of meat, milk or eggs (Broom, 2011). Earlier, some thinkers criticised this Cartesian point of view. We can cite Bentham (1781) and Rousseau (1754) for redirecting the question from animal reasoning to animal suffering or Thompson (1851): a pioneer in describing human-animal interactions who argued for different forms of intelligence. In 1952, Schweitzer was honoured with the Peace Nobel Prize for defending his idea of "Reverence for life" ("*Ehrfurcht vor dem Leben*"), which consists in respecting any kind of life (plants, animals, humans; for an illustration see the quotation beginning this chapter). This contributed to a decisive turning point in ethics and animal rights (Sambraus & Steiger, 1997). Since 1997, the European Union acknowledges animals as sentient beings (Boissy & Erhard, 2014; Broom, 2010b), defined as individuals with some ability to "evaluate the actions of others in relation to itself and third parties, to remember some of its own actions and their consequences, to assess risk, to have some feelings and to have some degree of awareness" (DeGrazia, 1996). Today, animal welfare has become a distinct objective set by the Food and Agricultural Organization (FAO) of the United States. It is considered

a necessary contribution to sustainable agricultural and economic development and to food security and human nutrition (Buller et al., 2018). However, it has been a long road to achieving the acknowledgement of animal welfare as a field of science (Fraser, 2008).

1.1.2 How animal welfare became a research topic

A critical event in the acknowledgment of problems associated with industrial farming was the publication of *Animal Machines* (Harrison, 1964). Harrison revealed the living conditions of intensive animal husbandry to the public and this recognition directly influenced the British government to create the Brambell Committee (Duncan, 2006). Notably, this committee highlighted the necessity to allow freedom of movements in intensively farmed animals (i.e. the ability to turn around, groom themselves, get up, lie down and stretch their limbs; Brambell Committee Report, 1965). From this emerged the concept of the "five freedoms" defined as follows: (1) freedom from thirst, hunger and malnutrition; (2) freedom from discomfort and exposure; (3) freedom from pain, injury and disease; (4) freedom from fear and distress; (5) freedom to express normal behaviour (Webster, 1994). As outlined by Duncan (2020), the Brambell Committee was farsighted in urging scientists to describe "feelings" of animals. Indeed, this committee defined welfare as following: "a wide term that embraces both the physical and mental well-being of the animal. Any attempt to evaluate welfare, therefore, must take into account the scientific evidence available concerning the feelings of animals [...]"(Brambell Committee Report, 1965). One year later, the Society for Veterinary Ethology (renamed International Society for Applied Ethology after 1991) was funded in England and opened the doors for research in ethology aiming at improving animal welfare (Broom, 2016). However, it was not before the early 1990's that methods to measure behavioural and physiological changes as indicators of welfare became properly established (Mason & Mendl, 1993; Sandoe & Simonsen, 1992). The fact that the concept of animal welfare dynamically evolved owing to the diversity in opinions (Fraser, 2008) might explain this timeframe to find a consensus. For instance, some pioneering authors considered that the primary objective was to understand the animal's point of view and its natural "behavioural needs" (Stolba & Wood-Gush, 1984). Others focused on the "biological functioning" and argued that poor animal welfare has similar consequences as poor fitness, which is mostly due to a failure of an individual to cope with its environment (Broom, 1986, 1991). Finally, other authors dared to place "animal feelings" (i.e. the subjective experience of their internal states) as a key aspect of reducing suffering in animal husbandry (Dawkins, 1980; Duncan & Dawkins, 1983). In order to avoid anthropomorphism (Burghardt, 2018; de Waal, 1999), the term "affective states" was later considered the most accurate for describing subjective experiences of animals. Duncan (1993) argued that animal welfare *only* depends on what the animal feels and on its mental health which appears closer to a definition of (human) psychological well-being. Cannon (1929) was officially the first to introduce the concept of affective states while referring to emotions and other feelings experienced as either pleasant or unpleasant rather than hedonically neutral (Fraser, 2008). For the sake of standardizing definitions of emotion, mood or feeling, Russell (2003) proposed to use the term of "core affect" to refer to "a neurophysiological state that is consciously accessible as a simple, non-reflective feeling that is an integral blend of hedonic (pleasure–displeasure; also called valence, ranging along a negative-positive axis) and

arousal (sleepy–activated) values". This "core affect", also described as a "raw feeling", varies as a single point on this two-dimensional space of valence and arousal at a given moment (Russell, 2003) and has been integrated into animal behavioural research (Mendl et al., 2010). As a result, the term "affective states" comprises of moods –the free-floating affect on the long term of an individual– and emotions –short-lived affective reactions directed towards a stimulus (Paul et al., 2005). More recently, some applied ethologists claimed that animal well-being should not only focus on the absence of negative affects but also (and even predominantly) on the presence of positive ones (Boissy et al., 2007; Burgdorf & Panksepp, 2006; Yeates & Main, 2008). In particular, animal welfare could be about offering conditions or situations that elicit "liking" states in farm animals (Gygax, 2017). As a result, affective states are nowadays central in the modern concepts of animal welfare which focuses on the quality of life in farm animals (McMillan, 2000; Webb et al., 2018; Yeates, 2016).

1.1.3 A definition of animal welfare centred on the individual and its affective states

Despite the various interpretations of animal welfare that emerged across time and currents of thought (Fraser, 2008), a general consensus has emerged which consists in acknowledging farm animals as individuals with their own needs (Broom, 2010a; Winckler, 2019). Personality research can represent a good framework for doing so (Finkemeier et al., 2018) because it is an established field for studying individual differences in the animal kingdom (Roche et al., 2016). However, it is only recently that some authors called to attribute personality to farm animals (Boissy & Erhard, 2014; Finkemeier et al., 2018; Puppe et al., 2012; Richter & Hintze, 2019). Finkemeier et al. (2018) reviewed the research on individual differences in farm animals and highlighted the discrepancy between the effort of farm animal researchers to use similar methodological approaches as those performed in behavioural ecological studies and the use of alternative terms (e.g. coping or temperament) rather than the personality concept itself. This practice can be considered as counterproductive because it might reinforce the vision that farm animals are an "extra" category of animals that do not deserve a personality. As a result, acknowledging and investigating personality in farm animals may enhance our readiness to improve their living conditions which could be beneficial for their welfare. Throughout this thesis, when talking about individual differences, I will focus on personality because it is the most used concept for studying individual differences in behaviour and physiology (Roche et al., 2016).

Thus, I decided to use a definition of welfare which places the individual as central element and which has the merit of integrating the presence of affective states: "Welfare is the state of physical and **mental health** resulting from the process of behavioural and physiological adaptation when coping with environmental challenges, and the associated **subjective experiences and emotional evaluation**, all in the light of **individual** and/or cognitive needs and abilities" (Puppe et al., 2012).

1.1.4 Affective states are produced by the brain

Studying affective states blows a fresh breeze not only into animal welfare research but also in the whole field of ethology. Indeed, it re-orientates focus back to proximate mechanisms (i.e. physiology and development) of behavioural control (Gygax, 2017) which have been overlooked in favour of ultimate mechanisms (i.e. consequences on fitness at the group or species level of a behaviour) with the emergence of behavioural ecology in the 1970's (Alcock, 2003). The field of affective neuroscience (i.e. the science of affective states) aims to explain the evolution of mammalian brains by demonstrating the existence of common neural substrates of wanting, liking or decision-making (Panksepp, 1998, 2000). Those systems are ruled by the "law of affect", suggesting the existence of a motivation system promoting approaching pleasant/rewarding stimuli and avoiding unpleasant/punishing stimuli (Cabanac, 2002; DeCatanzaro, 1999; Panksepp, 1998). In particular, in mammals, seven basic emotional systems (four positive: seeking, lust, care, play; three negative: rage, fear, panic) have been identified and matched with key brain areas and key neuromodulators (reviewed in Panksepp, 2011). Short-termed affective states (i.e. emotions) are major in the process of behavioural control because they serve in the process of decision-making ("wanting") and have feedback effects after an outcome has been evaluated ("(dis-)liking") in respect to an expected goal (Gygax, 2017). Mechanisms occurring during and at the origin of emotional reactions are a central topic in this thesis, therefore I will focus only on emotions.

Measurements of changes in affect are assumed to indicate whether farm animals experience a situation as pleasant or unpleasant. Accordingly, we could design optimal environments and develop best practices of care for improving their welfare (Duncan, 2020). However, because affective states take place in the brain, studying them non-invasively is very demanding. Few methods have been recently developed to measure cerebral activity in freely-moving farm animals such as functional near-infrared spectroscopy (fNIRS) which evaluates haemodynamic changes in specific brain areas. This method already permitted to distinguish emotions of different valences in goats (Gygax et al., 2013). However, further research is needed to validate this technique because results seem to be heterogeneous (Gygax & Vögeli, 2016; Raoult & Gygax, 2018; Vögeli et al., 2014). Similarly, the use of electroencephalography (EEG) which allows recording global neural activity shows the advantage of a high temporal resolution for studying short-termed reactions (in horses: D'Ingeo et al., 2019; Rochais et al., 2018; in pigs: Rault et al., 2019). Nevertheless, applied researchers did not wait for the emergence of those cutting-edge methods to investigate affect in farm animals. Indeed, one can indirectly assess affective states because they are often accompanied by peripheral physiological changes and result most of the time in one behavioural output (Gygax, 2017). Developing measurable indicators through behavioural, physiological and cognitive changes (i.e. using a componential view, see section 1.2.2 from page 8) that characterize an emotional reaction is therefore a field in progress since two decades in farm animal research (Paul et al., 2005).

To conclude this first section, personality and emotions are highly topical issues in animal welfare research and investigating their mechanisms are expected to be relevant to improve the welfare of farm animals.

1.2 Studying personality and emotions to improve animal welfare

1.2.1 Personality, multidimensionality, proximate mechanisms and animal welfare

Personality is defined as a correlated set of behavioural and physiological traits that are consistent through time and situations within individuals (Gosling & John, 1999). Despite this objective definition and pioneering work on individuality and group selection (Hull, 1980; Maynard Smith, 1964; Maynard Smith & Price, 1973), it took several decades to acknowledge that personality in non-human animals exists and can be based on a similar construct as human personality (Gosling, 2001; Gosling & John, 1999; Whitham & Washburn, 2017). In human research, the "Big Five" are acknowledged as the five main dimensions of personality: openness, agreeableness, extraversion, neuroticism and conscientiousness (John & Srivastava, 1999). Inspired from this "Big Five" model, a comparable model with five dimensions (i.e. exploration, aggressiveness, sociability, boldness and activity) has been proposed to study non-human animal personality (Réale et al., 2007). Indeed, the dimension of openness is similar to the dimension of exploration, agreeableness to aggressiveness, extraversion to sociability while neuroticism might include boldness and activity (Finkemeier et al., 2018; Gosling & John, 1999; Réale et al., 2007). Concerning conscientiousness which has been argued to be unique to great apes (Gosling & John, 1999), first investigations show the potential existence of this trait in other species which could be divided in several components including impulse control, order, or industriousness (Delgado & Sulloway, 2017). Another well-established concept closely linked to the concept of personality, is coping and has also proven its relevance to understand individual differences in behaviour and physiology (Cannon, 1929; Koolhaas et al., 1999). Coping is defined as the behavioural and physiological efforts to master a stressful situation (Koolhaas et al., 1999). The view that coping might be another personality dimension (Finkemeier et al., 2018; Koolhaas & van Reenen, 2016; Zidar et al., 2017) will be adopted throughout this thesis. Coping styles can be determined by classifying individuals along a continuum where "proactive" (also called "high reactive") subjects show strong responses to stressful stimuli while "reactive" (also called "low reactive") subjects respond more passively (Koolhaas et al., 1999; Roche et al., 2016). Those extreme types of behavioural reactions have been shown to be associated with distinct physiological reactions: for example, a proactive individual will show a higher sympathetic activation of the autonomic system while a reactive individual shows an increased activation of the hypothalamic pituitary adrenal (HPA) axis (Carere et al., 2010). Thus, in general personality (including coping) should be studied in a multidimensional framework (Finkemeier et al., 2018; Koolhaas & van Reenen, 2016; Zidar et al., 2017).

Researchers in behavioural ecology invested a lot of effort in studying ultimate mechanisms that can explain the maintenance of individual variability at the population level. This resulted in a variety of frameworks to study how different personality-types coexist at the population level (McElreath & Strimling, 2006; Sih et al., 2015; Wright et al., 2019). However, animal welfare researchers might be more attracted to understanding the proximate mechanisms of individual differences, especially in cerebral processing. Indeed, one of the new challenges for

animal welfare research is knowing how to manage individuals with different perceptions of their environment rather than simply knowing how different sub-groups coexist (Boissy & Erhard, 2014; Bushby et al., 2018; Finkemeier et al., 2018; Puppe et al., 2012; Richter & Hintze, 2019). Similarly to the field of human psychology, understanding personality or individual differences in emotional reactivity (i.e. "affective styles") at the neurophysiological level may be necessary to promote well-being (Davidson, 2004; Montag & Panksepp, 2017). For example, the factor neuroticism predicts some affective disorders (e.g. depression) in humans (Lahey, 2009) and further research might help to develop individualized care to treat those disorders (Montag & Panksepp, 2017). The first studies on individual differences in neurophysiology to explain personality emerged with Gray's reinforcement sensitivity theory (RST: Gray, 1973). This framework is based on the motivational system from which various personality traits are supposed to emerge (Gray, 1973). Indeed, individual differences in behaviour reflect the physiological variations in the sensitivity to stimuli associated with positive or negative reinforcement: for example, impulsive individuals are more sensitive to reward and may more often approach positively-perceived situations even with the presence of punishments (Depue & Collins, 1999). A revised version of the RST theory appeared later (Gray & McNaughton, 2000) and proposed the existence of three independent systems regulating motivation: the behavioural activation system (BAS: governing approach behaviour to rewarding stimuli), the flight-fight-freeze system (FFFS: governing avoidance behaviour to aversive stimuli), and the behavioural inhibition system (BIS: resolving approach-avoidance conflict situations when BAS and FFFS are activated, such as in situations of novelty). Interestingly, there is support for the existence of distinct neural structures regulating those systems (e.g. the amygdala, anterior and posterior cingulate, prefrontal ventral and prefrontal dorsal stream) that can become responsible for certain mental disorders (e.g. general anxiety or obsessive compulsive disorders; for a review, see Corr, 2009). Some authors consider that the RST theory opened the doors to the research field of personality neuroscience which nowadays consists in investigating the neural substrates of the "Big Five" (for a review, see Allen & DeYoung, 2016). Although the RST is based on rodent models (Berkman et al., 2009; Gray, 1970), this framework has not yet been used to explicitly study the neural substrates of non-human animal personality. Instead, first indications demonstrate that genetically identical mice can show individual differences in behaviour that are underpinned by individual differences in brain plasticity (Freund et al., 2015; Freund et al., 2013). In general this research field is at its early stage in non-human animals (Kempermann, 2019), and therefore there remains a need to better understand the neurobiological basis of personality.

Personality research can show broad applications with practical and economic interests that are indirectly related to animal welfare (reviewed in Finkemeier et al., 2018). Since differences in personality inherently include individual differences in physiology, it is not surprising to note that individual differences in personality can reflect individual differences in immunity, performance or metabolic rate (Biro & Stamps, 2008; Carere et al., 2010; Finkemeier et al., 2018; Holtmann et al., 2017). Those insights could be used to improve group management practices or breeding policies. For instance, due to the moderate heritability of some personality traits (e.g. docility) in farm animals and because those traits can improve their performance (e.g. milk production in dairy cattle or training in horses), the selection of docile personality types is already integrated in breeding objectives in some countries (e.g. in cattle and horses: Gibbons,

2009; König von Borstel et al., 2011). Another example could be the landmark studies on coping styles in pigs. Coping has long been acknowledged as very relevant for animal welfare (especially through the "biological functioning" view: Broom, 1986) because farm animals have to constantly cope with many challenging situations (e.g. regrouping, housing, certain handling practices: Finkemeier et al., 2018). In pigs, coping style is usually investigated using the *Back-test*, where a piglet is turned on its back and its attempts to free itself (the struggle intensity) from this aversive situation is measured in terms of latency, frequency and duration (Finkemeier et al., 2018; Hessing et al., 1993). Many studies showed that interactions between coping and general health and/or environment have implications in pig husbandry and management (e.g. Bolhuis et al., 2006; Ruis et al., 2001; Ruis et al., 2002). For instance, Bolhuis et al. (2006) showed that providing straw reduced gastric lesions in low reactive pigs but not in high reactive pigs. Moreover, enriched environments led to higher feed intake but only high reactive pigs gained weight. This study demonstrates that individual preferences in enrichment can be partly addressed by knowing the coping styles of pigs and that this may represent immediate benefits for the farmers. Based on those examples, personality research might be considered as appropriate to be implemented with precision livestock farming (Berckmans, 2017), since it shows high potential to allow individualized (medical) care and optimal monitoring of farm animals. However, as stated in the previous section, animal welfare is more a matter of what the animal feels, in particular of what the animal likes or wants (Gygax, 2017). In her review, Franks (2019) states that understanding individual differences in motivation could enable distinguishing between wants that should be accommodated to improve welfare and wants that should be changed to improve animal welfare. As suggested in the previous paragraph, those individual differences in motivation may have a neurophysiological basis that could be worthy of exploration in farm animals.

Methods to investigate personality in farm animals have been recently reviewed by Finkemeier et al. (2018) and it seems that multidimensional frameworks are recommended. On one hand, Koolhaas and van Reenen (2016) proposed a three-dimensional model based on individual differences in coping (proactive vs. reactive response), emotionality (highly vs. lowly aroused response) and "sociality". The latter, also called "sociability" is the motivation to remain close to conspecifics (Koolhaas & van Reenen, 2016) and can be measured through reactions during a separation test (Réale et al., 2007). However, emotionality seems to have neither a standardized definition (also called emotional reactivity: Boissy et al., 2005; Savage & Eysenck, 1964), nor standardized methods to be assessed (reactions to novelty: Archer, 1973; to threatening stimuli: Leliveld et al., 2017; or to a challenge: Koolhaas & van Reenen, 2016). On the other hand, the framework of Réale et al. (2007) might be more comprehensive than the one of Koolhaas and van Reenen (2016) which may explain why it is recommended for research in farm animals (Finkemeier et al., 2018; O'Malley et al., 2019). For example, in this framework, emotionality can be used as a synonym for fearfulness (Donald et al., 2011; Gosling, 2001; Koolhaas & van Reenen, 2016) a personality trait that might correspond to boldness (Réale et al., 2007). According to Carter et al. (2013) boldness refers to the response to a risky-situation when faced alone and it seems that reactions towards novel object, human or environment are the most common tests used in farm animals to assess their boldness (Finkemeier et al., 2018). However, the interactions with a novel object or environment can additionally reflect individual differences in

exploration (Réale et al., 2007). Finally, it is also possible to assess individual differences in general activity and aggressiveness (i.e. an individual's agonistic reaction towards conspecifics) in various farm animals (for a review, see Finkemeier et al., 2018). Moreover, integrating the study of coping into the five-traits model might contribute to obtain a comprehensive overview of farm animal personality (Finkemeier et al., 2018). We followed this recommendation in Study 2.

To conclude this section, studying personality in farm animals is promising for a better understanding of their individual needs. In order to do so, it is important to use multidimensional models and to develop new approaches to understand the neural substrates of personality. This is what our Study 2 aimed at.

1.2.2 Emotions, the componential view, appraisal and animal welfare

As previously demonstrated, the study of affective states is necessary to understand what animals like and want and therefore can help improving their welfare. Moreover, core affect seems to be a central issue in the study of emotional reactions (Mendl & Paul, 2020). Indeed, any emotional episode typically begins with an abrupt change in core affect in response to a certain event (Russell & Barrett, 1999). Animal emotions are defined as intense and short-lived affective responses to an event and are mostly accompanied by neurophysiological, behavioural, cognitive and subjective changes (Désiré et al., 2002). The first part of the definition outlines the short-term aspect of emotions: they differ from moods which hold for the longer term. As already explained in section 1.1.4 (page 4), emotions take place in the brain but it is possible to comprehensively characterize them with the use of a componential view (Paul et al., 2005). This is implied with the final part of the definition which outlines a combination of objective indicators reflecting behavioural, physiological and cognitive outputs during an emotional reaction.

Perhaps the most controversial part in the definition of emotion is the existence of subjective changes which pre-supposes the ability for the subject to be aware of its emotions (Panksepp, 2005). This presupposition cannot be tested yet because non-human animals cannot verbalize how they feel but this should not hinder research on their emotions, since even humans can experience emotions without being aware of them (Dawkins, 2015; Le Neindre et al., 2017). Indeed, humans, just like non-human animals, can show "unconscious, intuitive" reactions towards an event (Arnold, 1960a). This reflects complex interactions between emotions and appraisal, defined as the way an individual interprets and evaluates a situation or stimulus. Appraisal theories have been very influential in the field of human psychology for understanding the mechanisms of emotions (starting with Arnold, 1960a, 1960b). An individual appraises a situation by using a series of stimulus checks of this situation such as its novelty, valence, pertinence to individual's expectations, and the individual's capacity to cope with the situation (Lazarus, 1993; Schachter & Singer, 1962; Scherer et al., 2001). This implies that the same situation can be appraised differently between individuals, thus the appraisal framework may be a basis for studying emotional subjectivity (see next section). As an outcome of these stimulus checks, the human subject is able to label an emotional episode only at the end of this process (Scherer & Moors, 2019). However, because this verbalization step (self-report) can bias the results in humans (Tsuchiya et al., 2015), it is necessary to include objective indicators (i.e. behavioural outputs, physiological responses and motor expressions) of emotional reactions as well (Scherer

& Moors, 2019). In other words, the componential view seems to be also valuable for the study of human emotions (Larsen et al., 2008). Arnold is seen as a pioneer for having laid the basis of modern considerations on "automatic" (i.e. not necessarily conscious) appraisals (Gendron & Barrett, 2009; Kappas, 2006) which could refer to the neurophysiological mechanisms regulated by the peripheral nervous system (PNS). Indeed, emotional reactions are characterized by changes in activity of both sub-systems of the PNS: the somatic and autonomic nervous systems (respectively SNS and ANS; Briefer, 2012; Larsen et al., 2008). On one hand, the SNS activity can be reflected by changes in motor expressions (i.e. facial, vocal and gestural changes). For example, most of the facial musculature is innervated by the facial nerves whose afferent fibres are situated subcortically in the brainstem (PNS; Larsen et al., 2008). As a result, some studies on the SNS activity could match several facial expressions with some discrete emotions (e.g. disgust, sadness: Larsen et al., 2008). On the other hand, the ANS activity is more difficult to grasp because it results from the complex interactions between the sympathetic ("fight-flight" function) and parasympathetic (also called vagal; "rest-digest" function) systems (Scherer & Moors, 2019). This complexity is heightened by the possibility that the experience of emotions causes peripheral changes (because the brain sends efferent signals to the periphery) while peripheral changes may contribute to the experience of emotions (because the brain receives afferent signals from the periphery; Larsen et al., 2008). Interestingly, this issue reflects the debate on whether appraisal causes or is a consequence of emotions. The ANS can be assessed by measuring activity of dually (i.e. from both: sympathetic and vagal systems) innervated organs such as the heart (Larsen et al., 2008). However, it is difficult to identify emotion-specific autonomic patterns: the review of Kreibig (2010) showed differences in ANS activity that were related to the arousal of specific emotions but not to their valence. Indeed, putative sympathetic responses were associated with high-arousal emotions and parasympathetic responses were associated with low-arousal emotions (Kreibig, 2010; Porges, 1995; Scherer & Moors, 2019). In other words, Kreibig (2010) could not confirm the existence of different profiles of physiological response that would allow a distinction between different basic emotions. An explanation might be that the study of (continuous) activity of the ANS cannot be fitted into a framework of discrete (categorical) emotions (Scherer & Moors, 2019). All this demonstrates that further research is needed to better understand how emotions and appraisal interact and correlate with physiological reactions (Scherer & Moors, 2019).

The componential view of emotions, combined with the framework of appraisal theories in non-human animals, produced valuable insights into their emotions (Désiré et al., 2004; Paul et al., 2005; Veissier et al., 2009; reviewed in Boissy, 2019). Nowadays, it seems that the framework with valence and arousal as the two main axes (Mendl et al., 2010, see section 1.1.2 from page 2) is established in research on farm animal emotions. While emotional arousal is well described, emotional valence remains the most difficult –although the most relevant for animal welfare– dimension to assess in animals (Mendl & Paul, 2020; Paul et al., 2005). Therefore the focus of this paragraph will be on briefly summarizing which methods are used to assess emotional valence in farm animals. I sorted those methods by component: behavioural, cognitive and physiological. First, the most traditional way to observe whether a stimulus is perceived as positive or negative is to measure the approach and withdrawal behaviours (Cabanac, 1992; DeCatanzaro, 1999). However, this method has limitations since one can observe some exceptions such as

aggression which is an approach motivation supposed to be associated with a negative affect (Carver & Harmon-Jones, 2009). Another example is that fear from a predator leads mostly to withdrawal motivation, however this can be transformed into an approach motivation toward sources of safety (Kelley et al., 2016). Those exceptions highlight the importance of understanding the motivation (or "wanting") that underlies behaviour (Gygax, 2017; Mendl & Paul, 2020). Second, various methods in the last decade have been developed to measure the cognitive outputs of emotional reactions such as the cognitive bias (Harding et al., 2004; Mendl et al., 2009) or the attentional bias (Crump et al., 2018; Lee et al., 2016) tests where the response toward an ambiguous event is measured. Third, as stated previously, being able to measure neurophysiological reactions (from the brain or the PNS) is also promising to better comprehend emotional valence. On one hand, methods for measuring the central nervous system (CNS) activity (such as fNIRS and EEG) are recent and have been already mentioned in section 1.1.4 (page 4). Even if those methods are promising because emotions occur in the brain, it seems that they cannot be yet replaced by the componential view of emotions. Instead, they could be a good complement to the other components which highlights the importance of using devices in freely-moving animals. In particular, combining CNS with PNS indicators might become more and more necessary in the future to understand better the interactions between the brain and the peripheral organs (Hagemann et al., 2003). On the other hand, some methods to measure the PNS activity have been developed in farm animals. The ANS activity is well-reflected by the cardiovascular activity and can be measured in farm animals (von Borell et al., 2007). Findings confirm the idea that in particular heart rate variability (HRV, which reflects vagal activity) is helpful to assess emotional valence (Krause et al., 2017; Reefmann et al., 2009b). The SNS activity is mirrored by facial expressions which are motor expressions of emotional reactions (Larsen et al., 2008; Scherer & Moors, 2019) and can also reflect emotional valence in non-human animals (Descovich et al., 2017; Waller & Micheletta, 2013). Interestingly, vocalisations can be also classified in the category of motor expressions happening during an emotional episode (Scherer & Moors, 2019) and have the specificity of reflecting a combined activity of the SNS and the ANS (Briefer, 2012; Manteuffel et al., 2004). Indeed, the voice parameters are under the influence of both the SNS which regulates the tension of the vocal tract muscles and the ANS which is involved in the regulation of respiration (Briefer, 2012). Briefer (2012) reviewed and summarized the potential bioacoustical parameters that are promising for assessing emotional valence. As a result, first studies which tested various hypotheses about the link between bioacoustics and emotional valence are appearing (Briefer et al., 2019a; Briefer et al., 2019b; Friel et al., 2019; Leliveld et al., 2016). In conclusion, some indicators of emotional valence seem to be already used (approach-avoidance behaviours, HRV measurements) whereas others are currently being established (facial expressions, bioacoustical features) or are needed (brain activity measurements) to be implemented in order to complete the componential view of emotions.

While fear was the most studied emotion for a long time (Forkman et al., 2007), it seems that the call of Boissy et al. (2007) has been heard since an increasing number of studies on positive emotional valence have been published. This should contribute to a better understanding of how positive emotions are regulated since it could be possible to distinguish what animals want from what they like (Gygax, 2017; Yeates & Main, 2008). Furthermore, Camerlink (2019) recently highlighted that non-intense emotional reactions remain a largely unexplored field in farm an-

imals. Indeed, stimuli of extreme valence may not be very representative of the everyday life of farm animals. Thus, research on emotions in farm animals, and especially on appraisal and emotional valence is far from complete. Therefore, componential approaches integrating both categories of neurophysiological parameters (CNS and PNS activities) should be considered and this is what we aimed in Study 3.

1.2.3 Personality and emotions: same underlying neural mechanisms?

As highlighted in the previous section, appraisal could form the roots of subjectivity (i.e. individual differences for experiencing emotions). Indeed, the appraisal of an event depends on the individual's expectation regarding the event and on its capacity to cope with this event (Lazarus, 1993; Schachter & Singer, 1962; Scherer et al., 2001). It is interesting to note that the concept of coping is included, suggesting that individuals with different coping styles will show different emotional reactions when facing the same stressful situation (Lazarus, 1993). The stress-response system and its impact on personality has been intensively studied (reviewed in Hengartner, 2017). In particular, individual differences in neuroendocrinological systems involved during stress (HPA axis and the ANS) have been shown to explain the different coping strategies and their correlations with some personality traits such as aggressiveness or boldness (reviewed in Hengartner, 2017). Interestingly, recent evidence show that baseline vagal activity might predict individual stress resilience or coping style (Carnevali et al., 2018; Krause et al., 2017). The anterior cingulate cortex has been proposed as a candidate structure responsible for individual differences in vagal tone (Carnevali et al., 2018). However, not every emotion elicits stress and coping has been shown to partly reflect the personality concept (see section 1.2.1 from page 5). In line with this, Hengartner (2017) states that not only the stress-response system but also the attachment system underlies the expression of personality and that both these systems overlap through common neural mechanisms (e.g. during oxytocin-mediated reactions to acute stress). Other authors emphasize individual differences in the regulation of monoamine neurotransmitters to explain differences in personality (Massen et al., n.d.). Dopamine levels can alter temperament (Cancela et al., 2001; Roberts et al., 2016), especially for traits related to exploration and novelty-seeking (DeYoung, 2013). Furthermore, individual differences in the metabolism of the serotoninergic system may account for differences in aggression (Buckholtz & Meyer-Lindenberg, 2008; Chester et al., 2015). Genetic studies on the polymorphism of monoamine receptors or transporters (Fidler et al., 2007; McCormack et al., 2009) and experimental manipulations of the monoamine systems (Abbey-lee et al., 2018; Silva et al., 2020) support the idea that individual differences in those systems underlie differences in several personality traits. Based on those findings, it is logical to expect that personality interacts with both emotional reactions and appraisal. For example individuals experiencing more positive emotions might show more approach behaviours in general, resulting in bolder individuals (more insights in Franks et al., 2014). Figure 1.1 (page 13) aims at illustrating the possible relationships between personality and behavioural control that is regulated by affective states (for more details on the feedback loops, see Gygax, 2017).

Some existing theoretical frameworks aim at explaining the affective basis of personality. On one hand, although the "Big Five" represent five dimensions that characterize an individual,

those dimensions are not purely independent and can correlate between each other (Erdle & Rushton, 2010; Musek, 2007). To explain the biological basis at the origin of the "Big Five", the hypothesis of a general factor of personality (GFP, also called the "Big One") emerged (Just, 2011; Musek, 2007). Interestingly, this "Big One" has been shown to correlate with affect, personal well-being and self-esteem (Musek, 2007). Even if the existence of the GFP remains controversial (Hengartner et al., 2017; Muncer, 2011; Weiss et al., 2011), it is interesting to note that there is growing evidence which shows associations between the "Big Five" and general positive and negative affect (reviewed in Reisenzein & Weber, 2009). For example, neuroticism is mostly a disposition to experience negative emotions, while extraversion is mostly a disposition to experience positive emotions (Reisenzein & Weber, 2009). On the other hand, as mentioned in section 1.2.1 (from page 5), the reinforcement sensitivity theory (RST) might be also an interesting framework to study the affective basis of personality. Indeed, the RST draws attention "not to the observed behaviours but to the internal, central states that underlie them" (Corr, 2009). Additionally, this theory distinguishes affect from motivation which might have the advantage of helping to disentangling core affect from "wanting" in the process of behavioural control. More concretely, the RST could explain why DeYoung et al. (2010) found associations between the volume of different brain structures and the Big Five using structural MRI. For example, extraversion was associated with the volume of the medial orbifrontal cortex which is involved in reward sensitivity while neuroticism was associated with structures involved in punishment sensitivity (DeYoung et al., 2010). Another advantage is that this theory is not mutually exclusive with the existence of a GFP, since Erdle and Rushton (2010) suggested that the motivational systems (BIS and BAS, see the RST in section 1.2.1) might be the neurological basis of the GFP. Interestingly, Kennis et al. (2013) reviewed fMRI studies on personality and showed that higher BAS scales are associated to activity of the ventral and dorsal striatum and ventral prefrontal cortex in response to positive stimuli while higher FFFS and BIS scales are associated to activity in the amygdala in response to negative stimuli. Therefore, the RST might represent a good framework to study the interactions between personality and emotions, as shown in Figure 1.1. Beyond the concept of personality, the development of techniques to measure brain activity during emotional processing has permitted the emergence of the concept of "affective styles" (Davidson, 2004). Affective styles refers to consistent individual differences in emotional reactivity and regulation (Davidson, 1998). The prefrontal cortex and the amygdala are acknowledged as major structures involved in affective styles and as relevant to study for well-being (Davidson, 2004; Davidson & Irwin, 1999). More strikingly, pioneers in this field showed that affective styles can be predicted by an individual's cerebral asymmetries during baseline activity (Davidson & Fox, 1989). Recently, indications show that the "Big Five" are also underlain by cerebral asymmetries (Allen & DeYoung, 2016; DeYoung et al., 2010). Based on this and on the complex interactions between core affect, motivation and behaviour (Gygax, 2017), one could expect that affective styles are closely linked to personality (see Figure 1.1). More interestingly, the observation of asymmetries in behaviour can give insights into whether those cerebral asymmetries reflect differences between individuals or between emotions (Rogers et al., 2013). Therefore, the study of cerebral asymmetries is expected to be promising for understanding the common neural mechanisms underlying emotions and personality.

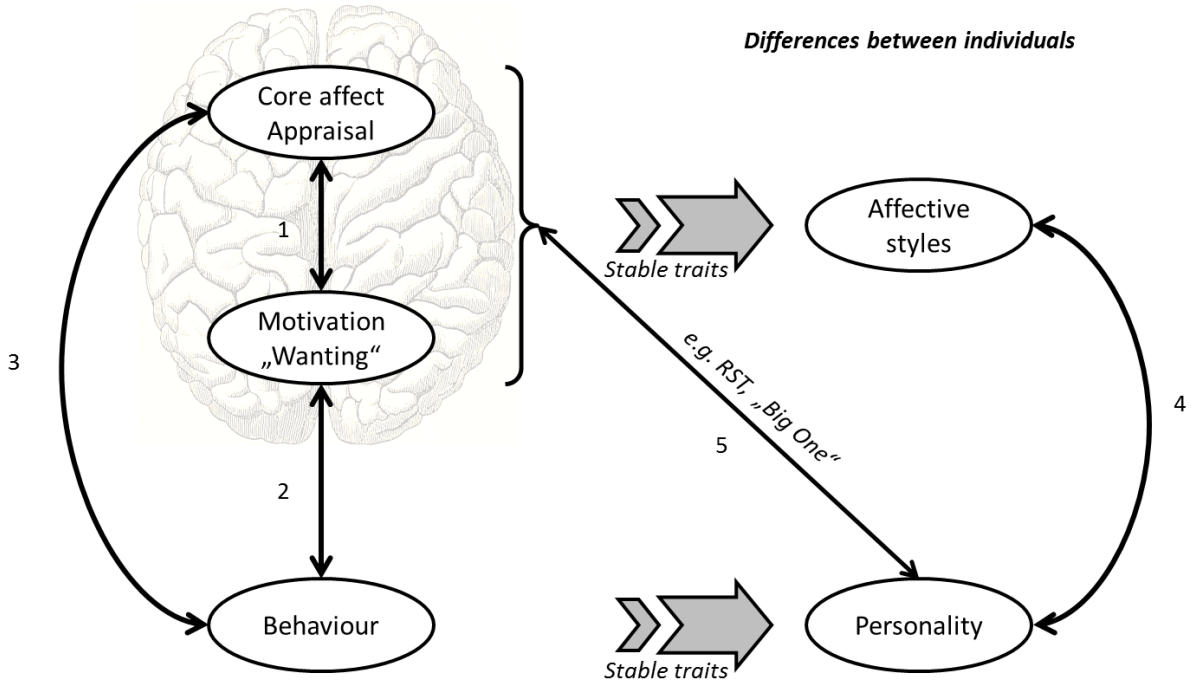

Figure 1.1: *Overview of the supposed links between the core concepts of this thesis and of how they interact with behaviour: core affect, "wanting", personality and affective styles.*

Several recent reviews focus more precisely on feedback loops (see arrows 1, 2 and 3) between core affect, motivation and the resulting behavioural output (Burghardt, 2019; Gygax, 2017; Mendl & Paul, 2020). The componential view of emotions consists in combining direct observations of behaviour with indirect measurements of cerebral processes (e.g. involved in (3) core affect or (2) motivation) reflected by cognitive or neurophysiological changes (for more details, see section 1.2.2 from page 8). Differences between individuals can be described in behaviour and in affect (for instance via the observations of stable traits through time, see big right pointing arrows) which can be studied in the context of personality and affective styles, respectively (see text for more details). Given the interactions between core affect, motivation and behaviour, one could as well expect that affective styles and personality are linked (4). The reinforcement sensitivity theory (RST) provides predictions on the affective and motivational basis of personality while a general factor of personality (or "Big One") might explain the affective basis of personality (see text for more details). Both concepts are used here as examples to illustrate the link between personality and core affect and/or "wanting" (5).

1.3 Laterality as an approach to study animal welfare

As the study of laterality can help gain insights into the neural basis of emotion and personality, it is considered as a promising approach to improve animal welfare (Leliveld et al., 2013; Rogers, 2010). The term laterality refers to the phenomenon of asymmetries of the brain and behaviour (Rogers et al., 2013). The existence of hemispheric asymmetries (i.e. cerebral lateralization) indicates that the two brain hemispheres differ in structure and in function. Since each hemisphere connects and controls the contralateral part of the body (Rogers et al., 2013), those asymmetries are reflected by lateralized everyday behaviours which can be observed non-invasively through motor and sensory side biases –i.e. behavioural lateralization. This non-invasiveness is undoubtedly the reason why the interest for studying behavioural lateralization in vertebrates grew in the last decades. The fact that behavioural lateralization is an indicator of cerebral lateralization and thus of the central nervous system (CNS) will be a key element in this thesis.

1.3.1 The discovery of hemispheric specializations

The lateralized brain has long being thought (and to some extent, is still thought: Chance & Crow, 2007) to be unique to human because of its close relationships with "higher order" cognitive functions such as tool use or language (Gatto et al., 2019). Broca (1861a) is widely regarded as the first to discover that lesions of the left (L) hemisphere caused aphasia, the loss of language abilities (but see Manning & Thomas-Antérion, 2011). This discovery was the birth of the concept of the L hemisphere controlling language function (Hervé et al., 2013) which has been validated with studies using brain-imaging techniques with high spatial resolution, such as functional magnetic resonance imaging (fMRI; Knecht et al., 2000; Mazoyer et al., 2014; Tzourio-Mazoyer et al., 2015). The term "hemispheric specialization" is used when one hemisphere is specialized in a certain function (in the latter example: L hemispheric specialization for language) and when it is manifested in the majority of the population within a species (Cai et al., 2013). For non-human animals, it took more than one century for the first pioneering works on cerebral lateralization in rats and chicks to be published (Collins, 1975; Rogers & Anson, 1979), despite early descriptions of asymmetrical convolutions in non-human mammals (Leuret & Gratiolet, 1839). Meanwhile, many studies showed shared patterns of hemispheric specializations across many taxa, such as a L hemispheric specialization for processing vocalisations (Ocklenburg et al., 2013; dogs even process human language in their L hemisphere: Andics et al., 2016) or a right (R) hemispheric specialization for spatial abilities (Rogers et al., 2013). All these efforts contributed to the fact that today hemispheric specializations are widely acknowledged in non-human animals, even including invertebrates (Anfora et al., 2011; Rogers et al., 2013). Nowadays, laterality is rather considered as a general principle of organization in the animal brain and this phenomenon is supposed to have brought many evolutionary advantages (Rogers & Vallortigara, 2015; Vallortigara, 2019). Indeed, laterality is hypothesized to improve brain efficiency: for example, the brain can perform more than one task at the same time (Güntürkün & Ocklenburg, 2017; Rogers et al., 2004) or can save energy during cognitive tasks (Frasnelli & Vallortigara, 2018). A variety of shared hemispheric asymmetries exists across vertebrates, however in this thesis I will only

focus on those with regard to emotional processing (i.e. emotional lateralization).

1.3.2 Hypotheses about emotional lateralization and affective styles

There are four main hypotheses on emotional lateralization which all emerged from human research: the R hemisphere hypothesis, the emotional valence hypothesis (also called the affective hypothesis), the approach-withdrawal hypothesis (also called the motivational hypothesis) and the BIS/BAS hypothesis which focuses on individual differences in emotional lateralization and derives from the latter. The affective and motivational hypotheses are very similar in their predictions; therefore they are often converged into one hypothesis which may explain why the literature concerning the number of hypotheses on emotional lateralization (two, three or four; see Ocklenburg et al., 2018) remains inconsistent. In this section, I will first present the predictions of the R hemisphere hypothesis; second I will explain the similarities and differences of both the affective and motivational hypotheses; and third I will explain why the BIS/BAS hypothesis has been used to explain individual differences in emotional lateralization.

On one hand, the first investigation of emotional lateralization was done by Highlings-Jackson (1874) on emotional speech, one decade after Broca's discovery. He found that patients with a L hemispheric impairment –and therefore suffering from Broca's aphasia– were still able to swear fluently and to blurt out emotional exclamations, such as "*Sacré nom de Dieu!*" (Broca, 1861b; Harris, 2019; Lindell, 2018). Those findings gave birth to the R hemisphere hypothesis stating a R hemispheric specialization for processing emotions (Lindell, 2018). However, this hypothesis seems to be specific to research on asymmetries of facial expressions in humans (for reviews, see Gainotti, 2018; Lindell, 2018). Indeed, there are many findings demonstrating a R hemispheric specialization for the recognition of facial expressions as well as for the production of unintended facial expressions of emotions in humans (for a review, see Gainotti, 2018), and even in non-human primates (for a review, see Lindell, 2013): the L hemiface (controlled by the R branch of the facial nerve) produces more intense expressions than the R hemiface (Lindell, 2018). Furthermore, recent findings suggest that the R hemispheric hypothesis might be only true for specific processes such as unconscious processing in "lower pathways" (i.e. subcortical areas, such as the amygdala: Gainotti, 2012; Killgore & Yurgelun-Todd, 2007; Prete et al., 2015; Sander et al., 2005; Schepman et al., 2016; Wildgruber et al., 2006). As explained in section 1.2.2 (from page 8), facial expressions can mirror the brainstem activity through the facial nerves. Thus, it might be not surprising that most of the studies on unintended facial expressions were in line with the R hemispheric hypothesis (Gainotti, 2012, 2018; Prete et al., 2015). All this contributed to the idea that the R hemispheric hypothesis is not necessarily mutually exclusive with alternative hypotheses (such as the emotional valence hypothesis) as it is classically considered (Killgore & Yurgelun-Todd, 2007; Prete et al., 2015).

On the other hand, the idea that opposite emotions (e.g. positive/negative or approach/withdrawal) are respectively processed by distinct hemispheres is relatively recent. This was first supported by observations of either behavioural asymmetries (Ahern & Schwartz, 1979; Schwartz et al., 1979) or of cerebral asymmetries during the experience of emotions (Davidson et al., 1979; Harman & Ray, 1977). The publication of Schwartz et al. (1979) seems to be the first reference to the emotional valence hypothesis stating that the L hemisphere processes

positive emotions while the R hemisphere processes negative emotions. In the same publication, these authors also formulated what is nowadays called the approach-withdrawal hypothesis: the L hemisphere mediates approach behaviours while the R hemisphere mediates avoidance behaviours. From this followed many studies that amalgamated approach motivation with positively experienced emotions or avoidance motivation with negatively experienced emotions (Harmon-Jones & Gable, 2018). Indeed, since most of the predictions of the emotional valence and the approach-withdrawal hypotheses can overlap, both hypotheses are often confounded (Davidson, 2001; Demaree et al., 2005; Ocklenburg et al., 2018). In a meta-analysis on human emotional lateralization, support was found for the latter hypotheses rather than for the R hemispheric hypothesis (Wager et al., 2003). However, it is possible to also distinguish the emotional valence hypothesis from the approach-withdrawal hypothesis (see Figure 1.2, page 17). For example, anger is a negative emotion involving approach motivation (Carver & Harmon-Jones, 2009; Harmon-Jones, 2004). Research on anger in humans supports the approach-withdrawal hypothesis (Harmon-Jones, 2004; Harmon-Jones & Allen, 1998) since this particular emotion has been shown to be associated with a greater activity of the L hemisphere. Nevertheless, in a comparative review across vertebrates on emotional lateralization, support was found for the emotional valence hypothesis rather than for the approach-withdrawal hypothesis: more studies showed a R hemispheric specialization for aggression (Leliveld et al., 2013, see Table 1.2, page 24). In section 1.3.5 (from page 24), I will show that using the emotional valence hypothesis for studying emotional reactions and appraisal is well suited. According to Harmon-Jones and Gable (2018), the core distinction between the emotional valence and the approach-withdrawal hypotheses relies on different emotional processes. As already stated by Killgore and Yurgelun-Todd (2007), several hypotheses might be true only at different cerebral levels and therefore could reflect "different facets of a complex distributed emotional processing system". For instance, the emotional valence hypothesis may rather describe affect and the valence with which a particular stimulus/situation is experienced (the appraisal of a negative or positive core affect), while the approach-withdrawal hypothesis may rather describe the motivation ("wanting") or the decision made to approach or avoid a stimulus/situation (Harmon-Jones & Gable, 2018), independently of the valence of this stimulus/situation (Harmon-Jones et al., 2013). Figure 1.2 has been done in an effort to illustrate this idea; the R hemisphere hypothesis is not represented because the review of Leliveld et al. (2013) and the meta-analysis of Wager et al. (2003) did not support it.

It is worth noting that the technique of EEG opened the possibility of widening the research on emotional lateralization (Larsen et al., 2008), especially for measuring individual differences in hemispheric activity (Levy, 1983). Early work on this topic showed that a greater R hemispheric activity during resting (baseline activity) is associated with depression (Henriques & Davidson, 1991; Schaffer et al., 1983) or with a more intense response during stressful situations (in human infants: Davidson & Fox, 1989; in macaques: Kalin et al., 1998). This led Davidson (1984) to argue for the existence of stable affective styles in humans that are associated with "stable differences in baseline measures of activation asymmetry in both hemispheres" (Davidson, 1992a, 1992b; Wheeler et al., 1993, see Figure 1.2). Those differences could result in individual differences in personality (Davidson, 2004, see Figure 1.2). In particular, affective styles have been combined with the revised reinforcement sensitivity theory (already explained in sec-

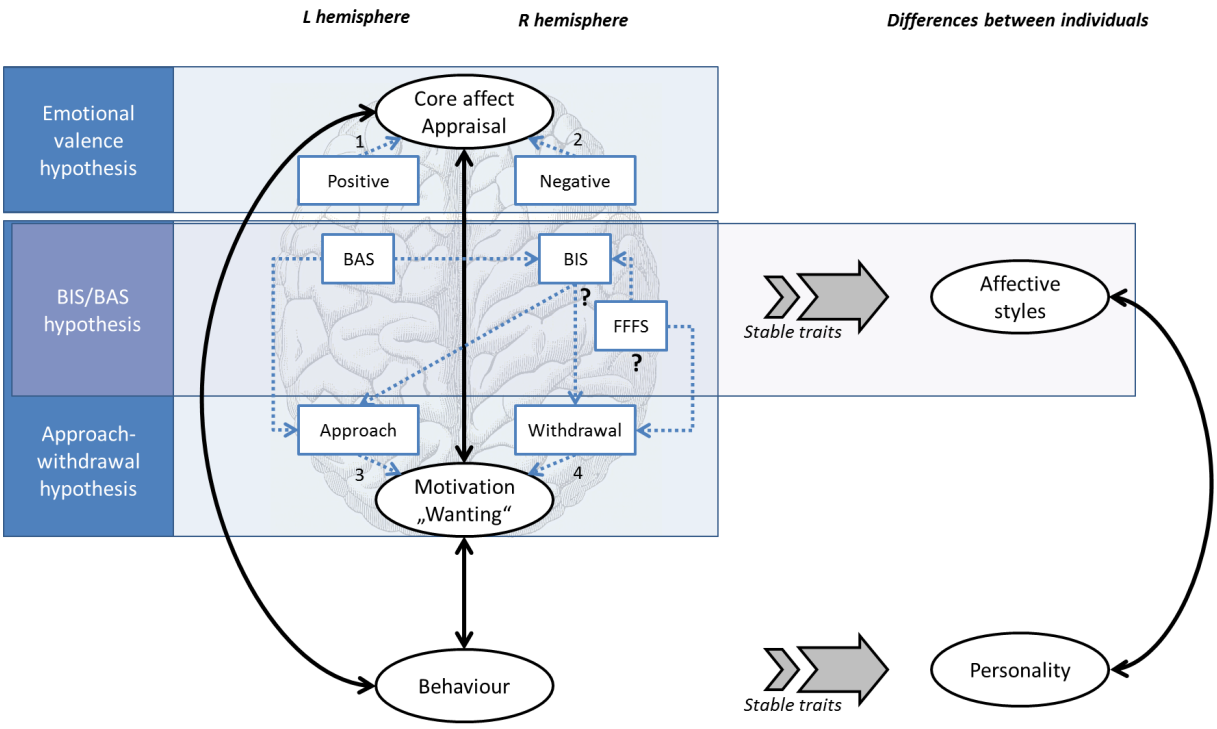

Figure 1.2: *Predictions of the different hypotheses on emotional lateralization (in blue) combined with Figure 1.1, page 13*

Solid lines represent the links between the core concepts of this thesis (in oval shapes), presented in Figure 1.1. Big right pointing arrows illustrate that stable traits in behaviour or affect result in the emergence of personality or affective styles (explained in Figure 1.1). Blue dotted lines link the predictions of each hypothesis (in rectangular shapes) to each proposed core concepts of this thesis. On one hand, the emotional valence hypothesis states that positive emotions are processed by the left (L) hemisphere while negative emotions are processed by the right (R) hemisphere. The emotional valence hypothesis seems to be well-suited to study core affect (see arrows 1 and 2) and especially how emotions are experienced (discussed in section 1.3.5, from page 24). On the other hand, the approach-withdrawal hypothesis states that approach motivations are processed by the L hemisphere while withdrawal motivations are processed by the R hemisphere. The approach-withdrawal hypothesis seems to be relevant for studying individual differences in motivation (see arrows 3 and 4), and therefore for studying personality (discussed in section 1.3.4, from page 20). The BIS/BAS hypothesis derives from the approach-withdrawal hypothesis and seems to explain individual differences in human affective styles rather than alternative hypotheses (see text for more details). The behavioural activation system (BAS) has been situated in the L hemisphere. However, findings showing a R hemispheric specialization for the behavioural inhibition system (BIS) or the flight-fight-freeze system (FFFS) remain inconsistent and are indicated by the questions marks (see text for more details)..

tion 1.2.1, from page 5; Gray & McNaughton, 2000). As a reminder, this theory states that there are three systems regulating motivation: the behavioural activation system (BAS: approach of rewards), the flight-fight-freeze system (FFFS: avoidance of punishments), and the behavioural inhibition system (BIS: resolving approach-avoidance conflicts). As the reinforcement sensitivity theory has been revised (which implied that the original BIS is more similar to the revised FFFS), it is important to note that the use of BIS or FFFS in the literature is inconsistent between

the original and the revised definitions (Gable et al., 2018). Findings show that individual differences in hemispheric activation better predict individual differences in (original) BIS/BAS traits than in negative/positive affective traits (Berkman & Lieberman, 2010; Gable et al., 2018; Sutton & Davidson, 1997). From this emerged the BIS/BAS hypothesis that makes similar predictions as the approach-withdrawal hypothesis: BAS/approach motivation is processed by the L hemisphere while original BIS or revised FFFS/avoidance motivation is processed by the R hemisphere (Gable et al., 2018; Ocklenburg et al., 2018; Sutton & Davidson, 1997, see Figure 1.2). Later, other authors found only a correlation between a greater L hemisphere activity and BAS scores/approach motivation (Coan & Allen, 2003; De Pascalis et al., 2013; Gable et al., 2018; Harmon-Jones & Allen, 1997, see Figure 1.2). The novelty of this model is to focus on stable individual emotional traits instead of emotions (Demaree et al., 2005), therefore this model can be considered as promising for studying the neural substrates of personality (DeYoung et al., 2010; Harmon-Jones & Allen, 1997). However, because this last hypothesis is very recent, one should be cautious with those findings. For instance, studies in accordance with this model have been recently questioned regarding the use of EEG (Reznik & Allen, 2018). Moreover, there is only little evidence associating avoidance motivation with greater R hemisphere activity (see the question marks in Figure 1.2; reviewed in Harmon-Jones & Gable, 2018). In a recent review, Gable et al. (2018) states that regulatory control (revised BIS) over both motivational systems (BAS and FFFS) seems to be correlated to greater activity of the R hemisphere (see the question marks in Figure 1.2) and should be more investigated with the help of fMRI. Finally, it is important to note that the model of BIS/BAS has until now only been tested in humans with the help of demanding brain imaging or neurophysiology techniques that are so far not commonly used in animals (but see: Kalin et al., 1998). Since we investigated behavioural lateralization, the BIS/BAS model was not considered in our experimental studies. Instead, I will demonstrate in section 1.3.4 (from page 20) that the approach-withdrawal hypothesis might be also adapted for the study of personality in animals.

1.3.3 Investigating behavioural lateralization

As demonstrated with the example of emotional lateralization, a direct measurement of cerebral asymmetries during specific tasks can be performed with the help of specific brain imaging or neurophysiology techniques. For instance, the technique of EEG can be used in free-moving humans (Ocklenburg et al., 2018; Reznik & Allen, 2018). In contrast, the development of similar non-invasive techniques in free-moving non-human animals is in its infancy (fNIRS and EEG; D'Ingeo et al., 2019; Gygax et al., 2013; Rochais et al., 2018) and demanding, therefore those studies remain scarce. As stated before, investigating behavioural lateralization has the main advantage of providing an indication of lateralized cerebral activity in a non-invasive way and in natural conditions. Even in humans, observations of behavioural lateralization have shown to be very informative and complementary to direct measurements of brain asymmetries (e.g. during kissing or embracing: Güntürkün, 2003; Ocklenburg et al., 2018; Packheiser et al., 2019). In practice, one can measure how individuals differ in strength (weakly vs. strongly consistent) and in direction (L or R) of laterality when performing a specific task. Like personality, behavioural lateralization is multidimensional: within an individual one can observe several types (motor or

sensory) of side biases varying in their degree (strength or direction) of lateralization when performing different types (e.g. cognitive, emotional) of tasks (Güntürkün, 2003; Tran et al., 2014). As stressed by Rogers (2017a), "any lateralization measure is not necessarily a fixed aspect of an individual or a species". For instance, the standardized accurate determination of handedness includes several tasks in humans (Healey et al., 1986; Oldfield, 1971; Steenhuis & Bryden, 1989) and occasionally in non-human primates (Anderson et al., 1996; Prieur et al., 2016; Wesley et al., 2002). The observation of multidimensional behavioural lateralization at the individual level demonstrates that similar proximate mechanisms regulate both personality and laterality. Indeed, maintaining individual differences in behaviour and physiology is advantageous and it seems that the mechanisms regulating personality (Sih et al., 2015) have the same origins as those regulating individual differences in laterality. Thus, a variety of trade-offs in behavioural lateralization patterns exists and results in differences between and within individuals according to external factors (Frasnelli & Vallortigara, 2018; Rogers & Vallortigara, 2015). For example, strong behavioural lateralization patterns have been shown to be associated with complex tasks (Fagot & Vauclair, 1991) or with complex organs (Keerthipriya et al., 2015, see the task complexity hypothesis that we used in the first study). Furthermore, different types of environmental factors have been shown to influence behavioural lateralization such as light exposition (Rogers, 1990; Zappia & Rogers, 1983), magnetic field (Malkemper et al., 2016), ocean acidification (Domenici et al., 2011; Lopes et al., 2016; Nilsson et al., 2012) or predation pressure (Ferrari et al., 2017). Hence, despite the existence of hemispheric specializations across species, one can still observe individual variations in behavioural lateralization on how an individual responds for example to unexpected stimuli, solves a cognitive task, monitors and escapes a predator, uses a tool or interacts with conspecifics. Thus, multidimensionality of laterality at the individual level should be taken into account –through testing with several tasks or several combinations of motor and/or sensory functions– to comprehend this complex phenomenon.

As previously mentioned, having a lateralized brain is advantageous (Rogers & Vallortigara, 2015) and many studies have reported how strong behavioural biases (reflecting strong cerebral lateralization) can be advantageous for individuals in a wide range of contexts across species (for a review, see Rogers, 2017b). However, there are potential costs for individuals being strongly lateralized such as making their behaviour more predictable by other animals (Chivers et al., 2016; Niven & Frasnelli, 2018). This may lead to exploitation of this predictable behaviour by conspecifics (i.e. during aggressive encounters) or by predators (i.e. when predicting escape bias of a prey; Niven & Frasnelli, 2018; Vallortigara & Rogers, 2005). Hence, apart from the advantages for individuals of being lateralized, laterality presents another intriguing aspect: it is often observable at the population level when a majority of individuals shows a bias in the same direction (Frasnelli & Vallortigara, 2018). To illustrate this, the famous example of human handedness (i.e. around 90% of the human population is R handed; Corballis, 2009; Papadatou-Pastou et al., 2019) is often cited. Moreover, Ströckens et al. (2013) recently showed that limb lateralization at the population level is a common phenomenon in vertebrates. The alignment of individual directional biases leading to behavioural lateralization at the population level offers advantages such as group coordination (Vallortigara & Rogers, 2005). Depending on the ecological context, individual-level or population-level behavioural lateralization may emerge (Frasnelli & Vallortigara, 2018). To account for this, models based on frequency-dependent se-

lection have been proposed to explain the evolution of lateralization in prey-predator (Ghirlanda & Vallortigara, 2004), in cooperation/competition (Ghirlanda et al., 2009; Pollet et al., 2013) or in fighting/mating interactions (Schnell et al., 2019). Again, these findings illustrate that the mechanisms regulating population of different behavioural lateralization styles are similar to those regulating populations of different personality types (Wolf & McNamara, 2012). Thus, knowing at which level (individual or population) a specific behaviour is lateralized allows for better understanding of how this behaviour evolved.

The most common method to investigate behavioural lateralization is to observe motor lateralization such as limb preferences during various motor tasks (Forrester, 2017; Ströckens et al., 2013; Versace & Vallortigara, 2015). This approach is attractive for the study of animal personality because stable motor biases for simple tasks are supposed to reflect consistent behavioural styles (Rogers, 2009) as will be further explained in next section (1.3.4). Alternatively, sensory lateralization is observable through eye, ear, nostril or antenna biases (Niven & Frasnelli, 2018; Rogers, 2017b; Siniscalchi, 2017). In particular, manipulating the use of sensory modalities has proven its worth for gaining knowledge on the precise role of each hemisphere during cerebral (e.g. cognitive or emotional) processes (Leliveld, 2019; Rogers, 2017b; Rogers & Vallortigara, 2019; Siniscalchi, 2017; Vallortigara, 2000). In section 1.3.5 (from page 24), I will explain why using sensory (visual, auditory, olfactory) lateralization is a promising avenue for the study of emotional processing, and especially of emotional valence (Leliveld et al., 2013; Morgante et al., 2010; Rogers, 2010).

1.3.4 Motor laterality and personality in non-human animals

As mentioned before, the observation of individual motor biases for simple tasks is considered ideal for linking laterality with personality. Consequently, studying motor laterality at the individual level might represent a fruitful approach for better understanding the mechanisms that underlie animal personality. In the previous sections, I outlined the importance of accounting for the multidimensionality of personality (see section 1.2.1 from page 5) and of behavioural lateralization (see previous section 1.3.3). Concerning the multidimensionality of personality, I have already introduced the five-dimensional model of Réale et al. (2007, see section 1.2.1). Accounting for the multidimensionality of motor laterality might consist in combining several types of motor biases. For example, by observing motor functions involving paired organs (such as limb preferences for stepping: Tomkins et al., 2010b; or for reaching food: Cameron & Rogers, 1999) as well as unpaired organs (such as tail postures: Laska, 1998; or neck position: Anderson et al., 2010, during resting). Motor biases for simple tasks are assumed to be "non-obligate, not determined by the functional differences between the hemispheres" (Rogers, 2009). In other words, they are suited for indirectly revealing individual differences in hemispheric *baseline* activities. This reminds us of the definition of affective styles (i.e. stable differences in *baseline* measures of activation asymmetry in both hemispheres) although affective styles can only be revealed by direct measurements of hemispheric activity. Similarly, the concept of "individual hemispheric dominance" can be defined as the more frequent use of one hemisphere over the other and is supposed to be easily observable through consistent behavioural lateralization patterns (Kinsbourne, 1997; Wright & Hardie, 2015). Indeed, recent studies in humans using

fMRI (Grabowska et al., 2012), EEG (Packheiser et al., 2020) or transcranial magnetic stimulation (TMS; van den Berg et al., 2011) validated the idea that the contralateral hemisphere to the dominant hand is generally involved in the motor control of the body, independently of the side (i.e. L handers show a stronger activation of the R hemisphere during manual motor tasks while R handers show a stronger activation of the L hemisphere during manual motor tasks). This concept of individual hemispheric dominance might represent an alternative to measurements of cerebral baseline asymmetries used in affective styles research, especially in freely-moving non-human animals. We used this approach in Studies 1 and 2 (see Figure 1.4, page 33). Individuals with opposite hemispheric dominance (i.e. with opposite stable motor lateralization patterns) are hypothesized to differ in their personality, emotional reactivity, or coping style (Rogers, 2009). When measuring individual hemispheric dominance through motor biases, it is important to investigate "simple" motor functions (Rogers, 2009) that are as emotionally neutral as possible. Indeed, on one hand, according to the task complexity hypothesis (see previous section), the more complex the task is, the more likely it is to observe a bias at the population level due to a hemispheric specialization related to postural, perceptual and/or cognitive processes (Fagot & Vauclair, 1991). Similarly, on the other hand, according to the hypotheses on emotional lateralization (presented in 1.3.2, from page 15), one could expect that the more emotionally laden the task is, the more likely it is to observe behavioural lateralization at the population level reflecting emotional lateralization.

Many studies in vertebrates have already investigated the link between motor lateralization and some personality traits. Table 1.1 (page 22) provides an overview of those studies. Commonly, individuals are distinguished in their lateralized motor patterns according to their biases in direction (R or L biased: see Table 1.1) or in strength (weakly or strongly biased). In order to standardize the overview in Table 1.1, the findings of each study were classified according to the definition of each five personality dimension given by Réale et al. (2007). The reason why coping is not included in this table is explained in the next paragraph. It must be noted that most of the studies cited in this section used only one parameter for motor lateralization (hand or paw preferences for one task) and did not systematically use a multi-trait assessment for personality (but see recent studies: Barnard et al., 2017; Found & St. Clair, 2017; McDowell et al., 2016). As a consequence, in most of those studies, a consistent motor bias (for only one motor function, such as hand preference for reaching food) was assumed to mirror a contralateral individual hemispheric dominance. It seems that most findings show that R biased individuals (assumed to have a L hemispheric dominance) are bolder and more explorative than L biased individuals (assumed to have a R hemispheric dominance; Table 1.1), which seems to support both the approach-withdrawal or the emotional valence hypotheses (Davidson, 1992b; Demaree et al., 2005). Evidence also shows that R biased individuals are more active, less aggressive, or more sociable (Table 1.1) than L biased individuals but more studies are needed to determine a clear pattern. For example, if aggressiveness increases with a L bias –R hemispheric dominance– across taxa, the pattern would support the emotional valence hypothesis. In general, even if both the emotional valence and the approach-withdrawal hypotheses are supported by the Table 1.1, one can consider the motivational model (approach-withdrawal hypothesis) as more appropriate to study personality. For instance, boldness or exploration traits reflect a general motivation to approach a risky stimulus or to explore a novel stimulus rather than the core affect of the individual.

In turn, the affective model (emotional valence hypothesis) might appear more appropriate for studies investigating long lasting affective states (moods; e.g. with the cognitive bias) and their interactions with laterality: L biased individuals seem to be more pessimistic than R biased individuals (Gordon & Rogers, 2015; Marr et al., 2018; Wells et al., 2017). It is interesting to note that both these hypotheses might help disentangling the interactions between mood and personality, which is not the topic here.

Furthermore, a substantial number of studies also suggest links between various personality traits and strength of laterality (Table 1.1). Notably, the associations suggested between boldness and strength of laterality seem to be inconsistent: bolder individuals can show either a stronger bias (Branson & Rogers, 2006; McDowell et al., 2016; Reddon & Hurd, 2009b) or a weaker bias (Barnard et al., 2017; Found & St. Clair, 2017). Therefore, it is also important to investigate the link between strength of laterality and personality in order to gain insight into a possible pattern.

Table 1.1: Overview of the animal studies linking motor laterality using the five personality traits model of Réale et al. (2007).

Trait	L bias	R bias	Weak bias	Strong bias	No association
Boldness	fish[1]	carnivores[2]	carnivores[9]	carnivores[11,12]	fish[14,15,16]
		primates[3,4,5,6]	ungulates [10]	fish[1,13]	primates[17]
		ungulates[7,8]			
Exploration		primates[4,5,6,18,19] *			primates[17]
					ungulates[10]
Activity	fish[21]	carnivores[22]		primates[20]	fish[14]
	primates[17]	primates[18]			
		rodents[23]			
Aggressiveness	birds[26]	carnivores[27]	carnivores[9,12]	primates[19]	fish[28]
	carnivores[24,25]		fish[21]		
Sociability		primates[18,29,30,31]	carnivores[9]	ungulates[32]	carnivores[12,22]
					fish[14]

Each study is classified according to which trait was investigated and whether it was associated with a left (L), right (R), weak or strong bias or whether no associations were found. [1]Brown and Bibost (2014); [2]Batt et al. (2009); [3]Hopkins and Bard (1993); [4]Hopkins and Bennett (1994); [5]Braccini and Caine (2009); [6]Cameron and Rogers (1999); [7]Larose et al. (2006); [8]Phillips et al. (2015); [9]Barnard et al. (2017); [10]Found and St. Clair (2017); [11]Branson and Rogers (2006) ; [12]McDowell et al. (2016); [13]Reddon and Hurd (2009a); [14]Irving and Brown (2013); [15]Byrnes et al. (2016a); [16]Dadda et al. (2007); [17]Watson and Ward (1996); [18]Gordon and Rogers (2010); [19]Fernández-Lázaro et al. (2019); [20]Tomassetti et al. (2019); [21]Chivers et al. (2017); [22]Barnard et al. (2018); [23]Glick and Ross (1981); [24]Schneider et al. (2013); [25]Siniscalchi et al. (2019); [26]Anderson et al. (2010); [27]Wells et al. (2019); [28]Reddon and Hurd (2008); [29] Westergaard et al. (2003); [30]Westergaard et al. (2004); [31]Vaughan et al. (2019); [32]Barnard et al. (2015)
* link between exploration and hand preferences in non-human primates has been reviewed by Rogers (2018)

As mentioned before, the study of coping belongs to personality research and is also relevant for animal welfare science. First, the R hemisphere is supposed to be involved in the physiological stress response involving the HPA axis (Rogers, 2010; for recent review, see Ocklenburg et al., 2016). This might explain findings showing that L motor biases are associated with a higher HPA axis reactivity in mice (Neveu & Moya, 1997) or with a higher risk of impaired activity of the HPA axis in macaques (Westergaard et al., 2003). Second, Rogers (2010) stated that directional biases

should give insight into coping styles. She suggests that the L hemisphere controls proactive behaviours while the R hemisphere controls reactive behaviours (Rogers, 2009, 2010). This hypothesis (sometimes called the proactive-reactive hypothesis: Barnard et al., 2018) supposes that R biased individuals have a more proactive coping style while L biased individuals have a more reactive coping style. As a consequence, Rogers (2010) suggested that behavioural lateralization should help identifying individuals with a higher vulnerability to stress which is important for animal welfare. However, coping is absent from Table 1.1, because it is difficult to standardize its definition across research fields and species. Indeed, it seems that in some studies a reactive coping style is used as a synonym of stress vulnerability although a coping style is supposed to reflect a strategy to deal with a stressful challenge rather than the success of the outcome of its response to that challenge (Colditz & Hine, 2016). For example, Barnard et al. (2018) found that dogs with a L bias showed higher expression of "stress-related behaviours" (such as more sitting or showing more lower posture) and concluded that dogs with a R hemispheric dominance may show a more reactive coping style and might be more vulnerable to stress, as predicted by Rogers (2010). However, some other "stress-related behaviours" that were associated with a L bias including frequent changes of state and an increased number of vocalisations might have been as well interpreted as a more proactive coping style. In contrast, cows using their L eye during social interactions (assumed to have a R hemispheric dominance) have been found to show more overt responses to restraint test (Phillips et al., 2015). Those findings have been interpreted as following: cows with a R hemispheric dominance show a more fearful temperament and therefore are more vulnerable to stress than cows with a L hemispheric dominance (Phillips et al., 2015). Again, this result could have been interpreted as a more proactive response for cows with a R hemispheric dominance which would contradict the proactive-reactive hypothesis. This inconsistent use of the concept of coping in the laterality's literature might be due to the possible misconception that proactive behaviours should be associated with calm and explorative behaviours combined with a positive cognitive bias while reactive behaviours should be associated with fearful and aggressive behaviours combined with a negative cognitive bias (Barnard et al., 2018; Rogers, 2010). Instead, proactive and reactive *emotions* seem to be involved in decision-making in a more complex way, as discussed by Gygax (2017). Additionally, strength of laterality may also reflect coping (Branson & Rogers, 2006; Byrnes et al., 2016b; Fernández-Lázaro et al., 2019; Morgante et al., 2007; Sullivan et al., 2012). In general, probably owing to the multi-faceted characteristic of coping which includes stress physiology and behaviour, findings about its link with laterality still remain inconsistent (Batt et al., 2009; Pereira et al., 2018; Vaughan et al., 2019; Westergaard et al., 2000; Westergaard et al., 2001; Westergaard et al., 2003; Westergaard et al., 2004).

To conclude this section, integrating the study of individual motor lateralization patterns into personality research is promising to substantially improve the understanding of the neurophysiological basis of personality. To obtain a comprehensive overview of those associations it is, however, necessary to account for the multidimensionality of both behavioural lateralization and personality. For this reason, we used this approach in the first and second studies. Furthermore, as the approach-withdrawal hypothesis seems the most adapted framework to study the associations between laterality and personality, we tested this hypothesis in Study 2.

1.3.5 Sensory laterality and emotions in non-human animals

Studying sensory laterality might be well suited to investigate the mechanisms of emotional processing. However, one cannot neglect the fact that motor lateralization patterns have been considered as valuable additional information on motor expressions of emotional reactions. For example, the use of the L forelimb reflects a stressful situation in horses (Siniscalchi et al., 2014), the direction of tail wagging predicts approach and withdrawal behaviours in dogs (Quaranta et al., 2007; Siniscalchi et al., 2013), lateralized ear postures can indicate frustration in sheep (Reefmann et al., 2009a), and hemimouth asymmetries reflect the type of vocalizations in infant monkeys (Wallez & Vauclair, 2012). Despite this, Leliveld et al. (2013) demonstrated in their review that most studies on emotional lateralization investigated sensory modalities. A possible explanation could be that the observation of sensory lateralization patterns gives insight not only into how the subject reacts to a stimulus/situation but also how it perceives this stimulus/situation. This distinction between perception and reaction to a stimulus could give insight into the mechanisms of proximate behavioural control. In this section, I will focus on visual laterality because it is the most studied modality in the context of emotional lateralization compared with other sensory modalities (Leliveld et al., 2013; Rogers, 2017b). Table 1.2 (page 24) summarizes the review of Leliveld et al. (2013) and illustrates why the authors found support for the emotional valence hypothesis rather than for alternative hypotheses. For instance, studies on eye preferences showed that food rewards are mostly viewed with the R eye (processed by the L hemisphere) while the L eye (processed by the R hemisphere) is mostly used during negative stimuli eliciting fear or aggression (e.g. Braccini et al., 2012; De Boyer Des Roches et al., 2008; Koboroff et al., 2008; Siniscalchi et al., 2010).

Table 1.2: Number of vertebrate species for which left (L) or right (R) hemispheric dominance has been showed according to the type of stimulus according to the review of Leliveld et al. (2013).

Stimuli	L hemisphere	R hemisphere
Fear	7	40
Aggression	4	18
Negative (subtotal)	11	**58**
Sex	4	5
Food	21	6
Socio-positive interactions	3	5
Positive (subtotal)	**28**	16

Fish taxa were excluded since the authors argued that this taxa seems to differ from other vertebrates in its lateralization patterns, probably due to different methodology used or different regulation mechanisms.

As outlined in section 1.2.2 (from page 8), using a componential approach is necessary to understand emotional reactions (Paul et al., 2005) and combining indicators of CNS and PNS activities might offer new perspectives for research on emotions (Hagemann et al., 2003; Larsen et al., 2008). The study of hemispheric asymmetries combined with other well-established indicators of emotions (e.g. approach/avoidance behaviours, heart rate variability measurements) might represent a first step in this direction. In line with the idea that observing sensory lat-

eralization patterns gives insight into how a subject perceives a stimulus, most of the studies on visual laterality showed that eye preferences preceded behavioural outputs according to the valence of the stimulus (i.e. approach of positive stimuli were preceded by R eye use and withdrawal of negative stimuli were preceded by L eye use: Austin & Rogers, 2007, 2014; De Boyer Des Roches et al., 2008; Kappel et al., 2017; Koboroff et al., 2008; Larose et al., 2006; Robins et al., 2018; Robins & Phillips, 2010; Siniscalchi et al., 2010; Versace et al., 2007). However since those same studies did not combine eye preferences (reflecting CNS activity) with physiological outputs (reflecting PNS activity) during emotional reactions (apart from few examples in dogs: Siniscalchi et al., 2013; and in horses: Smith et al., 2016), more research is needed to obtain a more accurate overview on how laterality interacts with emotions and appraisal.

Before using sensory biases (e.g. eye preferences) as indicators of CNS activity, it is important to know how sensory (e.g. visual) pathways are innervated in the species of interest. Visual laterality presents some advantages in species with laterally placed eyes and large monocular visual fields such as birds, rodents or ungulates (Hughes, 1977; Rogers, 2017b). In particular, the decussation of optic nerves into the contralateral hemisphere in those species is relatively high and well described (Herron et al., 1978; Rogers, 2017b; Vallortigara, 2000) and it can be assumed that, in these species, most of the visual inputs of an eye are processed by the contralateral hemisphere (Rogers, 2017b). Therefore, the observation of eye preferences is a direct observation of which hemisphere controls the response toward a stimulus (Rogers, 2017b). Moreover, with the prerequisite of a strong decussation degree, it appears that monocular viewing (achieved through occluding an eye) is an even more reliable method since one can test and compare the effect of the R vs. L hemispheres for a same stimulus (Rogers, 2017b). However, researchers rarely used this paradigm in the context of emotional lateralization (Rogers, 2017b).

As highlighted in section 1.2.2 (from page 8), the mechanisms of emotional valence are still not well understood, nevertheless the framework proposed by the emotional valence hypothesis shows interesting potential. Using such an approach assumes that the emotional reactions of a subject towards stimuli of different valence are influenced by the eye with which they are seen. As such, it would be appropriate to be able to focus on the valence, independently of the arousal. A possible solution would be to use the paradigm of emotional conditioning (as described in fish: Bisazza et al., 2000; Reddon & Hurd, 2009a). This paradigm consists in presenting similar artificial objects that have been preliminarily associated with stimuli of different valences. To my knowledge, only one study in mammals (horses) used a similar method to emotional conditioning: De Boyer Des Roches et al. (2008) used objects that were supposed to be associated with negative (white shirt similar to veterinarian shirt, observed with the L eye), novel (orange plastic cone, observed with both eyes) or positive (familiar food bucket but without food, observed with both eyes) situations. In this study, it was therefore more logical to interpret that the different reactions observed were due to the differences in valence rather than in arousal. In contrast, most of the studies on emotional lateralization test naturally arousing stimuli (e.g. Braccini et al., 2012; Siniscalchi et al., 2010), making difficult to distinguish emotional valence from arousal or other cognitive functions involved during the reaction towards a stimulus. Indeed, seeing either a food reward or a predator can lead to intense reactions of either positive anticipation or fear, respectively. Another argument for using emotional conditioning (i.e. artificial objects as stimuli) is that it allows for the observation of the subject's response independently of social interactions.

Indeed, due to the complexity of social interactions, both hemispheres are often simultaneously involved. For example, affiliative or agonistic interactions require the preliminary recognition of conspecifics (familiar or not) which is a R hemispheric specialization (Rosa-Salva et al., 2012). More strikingly, sexual behaviours that include courtship behaviours can require additional motor functions and therefore also involve both hemispheres (e.g. in birds reviewed by Rogers & Kaplan, 2019). This might explain why findings on sex and socio-positive interactions did not show a clear pattern of regulation by the L hemisphere (see Table 1.2, Leliveld et al., 2013).

To conclude this section, the potential for studying the lateralization of emotional valence has not yet been fully exploited. Indeed, using sensory lateralization combined with behavioural and physiological components would represent a valuable addition to research on emotions, not only for understanding emotional reactions but also appraisal. Moreover, there is a need for more studies testing monocular viewing (rather than measuring eye preferences) and/or using a paradigm of emotional conditioning. For this reason we used those combined approaches in Study 3.

1.3.6 Using behavioural lateralization for improving farm animal welfare

Even if research on laterality in the context of animal welfare is still in its infancy (for reviews, see Leliveld, 2019; Leliveld et al., 2013; Morgante et al., 2010; Rogers, 2010, 2011), adapting farm practices to the lateralization of farm animal should be the ultimate step for improving animal welfare (Leliveld, 2019). Before reaching this step, it is important to have preliminarily investigated which contexts or practices can influence the lateralization of farm animals. A first approach could be the study of behavioural lateralization at the group level in order to identify stressful situations. Indeed, previous research in husbandry relevant contexts has already shown that certain stressful housing conditions or husbandry practices influence behavioural lateralization. For instance, transport has been shown to induce a L forelimb use in horses (Siniscalchi et al., 2014) and in sheep (Robins et al., 2019) which supports the idea of a R hemispheric specialization for stressful reactions. However, there are many other potential stressful situations that could be identified through the observation of behavioural lateralization, but findings remain scarce and inconsistent. For example, reducing space availability in donkeys decreased strength of laterality (Zucca et al., 2011a) while intensive farming in cattle may increase strength of laterality (Phillips et al., 2003). Beyond using laterality as an indicator of stress, a second approach could be to induce laterality by changing those husbandry conditions or practices which could help reduce stress or even improve productivity. For the latter, striking findings in cattle showed that lateralized presentation of food on the L visual field improved milk productivity, supporting the idea of a R hemispheric specialization for gonadal function (Rizhova & Kokorina, 2005). Another example is that light exposure in chicks before hatching period induces strong visual lateralization which resulted in more stable social hierarchies in the group (reviewed in Rogers & Kaplan, 2019). Increasing light exposure before hatching in commercial conditions might therefore help laying hens to cope with social stress (Rogers & Kaplan, 2019). However, this hypothesis remains to be tested since it contradicts Riedstra and Groothuis (2004) who recommended to avoid light exposure before hatching in order to reduce feather pecking. A third approach could be to use behavioural lateralization as a predictor for the outcomes of social

(intra- and heterospecific) interactions. Indeed, understanding the dynamics of social groups is also a central issue in the management of farm animals (Foris et al., 2019). For instance, strong lateralization is associated with shorter fights in pigs (Camerlink et al., 2018a), with stable hierarchies in chicks (Rogers & Workman, 1989; Wichman et al., 2009) or with more dominant behaviour in cattle (Prelle et al., 2004). Those preliminary findings are promising for the management of intensively farmed animals for which damaging behaviours such as tail biting in pigs or feather pecking in hens remain major issues. Finally, studies on the lateralization of interactions between farm animals and humans could be used to determine from which side to approach and handle the animal, as suggested by findings in cattle (Goma et al., 2018; Phillips et al., 2015; Robins et al., 2018) or in horses (Farmer et al., 2010; Larose et al., 2006; Schuetz et al., 2017). Thus, more research using these three different types of approach might provide direct benefits for animal welfare in general.

In the previous sections, I explained how the study of emotional lateralization can help the understanding of personality and emotions; one could logically expect that this research should concretely help in improving animal welfare as well. First, individual lateralized motor biases have been already linked to individual stress reactivity or to specific personality traits (as mentioned in section 1.3.4 from page 20) which might be useful in group management of captive animals: individuals who are more sensitive to stress (e.g. in primates: Gordon & Rogers, 2015; Westergaard et al., 2003) or less sociable and more aggressive (e.g. in cats: McDowell et al., 2016) could be quickly identified and receive individualized care (Rogers, 2010). However, concerning farm animals it seems that the investigations of the link between motor laterality and personality have been so far restricted to the contexts of stress or health. For example, the link between the strength of laterality and stress reactivity has been already studied in sheep: strongly lateralized ewes were more stressed during a separation test (Barnard et al., 2015) and showed higher catabolic rate during pregnancy than weakly lateralized ewes (Morgante et al., 2010). Since coping can interact with general health (section 1.2.1 from page 5) and since motor laterality can reflect coping (section 1.3.4 from page 20), it is not surprising to see that links also exist between motor laterality and immunity (Morgante et al., 2007; Quaranta et al., 2006; Quaranta et al., 2008) or disease likelihood (Zucca et al., 2011b). In farm animals, there are some studies that have already linked behavioural lateralization with health issues such as lameness or mastitis (reviewed by Leliveld, 2019). Thus, the addition of individual behavioural lateralization patterns might be helpful not only for individualized health care but also for better group management (discussed in section 1.2.1 from page 5). Second, as highlighted in this thesis, more knowledge on affective states in farm animals should improve understanding of their mental experiences, which is necessary for improving their welfare. One can again outline that investigating sensory laterality can help give insight into how certain stimuli or situations are perceived (see previous section). For example, in the context of visual laterality, some findings in farm animals show differential involvement of brain hemispheres when seeing novel stimuli (e.g. Kappel et al., 2017; Larose et al., 2006; Phillips et al., 2015), threatening stimuli (e.g. Austin & Rogers, 2012; De Boyer Des Roches et al., 2008) or food rewards (e.g. Gygax et al., 2013; Rogers & Anson, 1979). However, its potential for improving welfare in farm animals has not been yet fully exploited (Leliveld, 2019; Rogers & Kaplan, 2019). As previously explained, using the emotional valence hypothesis might provide access to the core affect and to the appraisal of animals. For

example, one needs more studies similar to Reefmann et al. (2009a) who were able to show with the observation of lateralized ear postures that sheep are not necessarily in a positive state when novel (putative) attractive food is presented instead of regular food. Those kind of studies have the potential to enlighten subtle natural behaviours that are not yet well understood, especially "micro-behaviours" (e.g. ear movements: Reefmann et al., 2009a) that represent a promising topic for animal welfare research (Camerlink, 2019).

To conclude this section, studying laterality seems to be a very helpful approach due to its non-invasiveness and the ease with which it could potentially help improve animal welfare. Although this field is recent, there are already some studies in farm animals showing links between behavioural lateralization and stress physiology, housing conditions, husbandry and handling practices with possible recommendations to improve animal welfare. However, it seems that farm animals could benefit from more research on behavioural lateralization and on its interactions with personality and affective states. For this, Leliveld (2019) pointed out that, in particular, more theory-driven studies on laterality are required. Thus, this thesis aimed at showing the potential of using hypotheses on emotional lateralization (presented in section 1.3.2 from page 15) in order to help understanding of personality and emotional processing (discussed in sections 1.3.4 and 1.3.5) in pigs. This might be promising for both laterality research and animal welfare.

1.4 The pig as a model species

The domestic pig (*Sus scrofa*) is an ideal candidate to test hypotheses on emotional lateralization in the context of animal welfare. Indeed, this species is relevant for animal welfare research since it is the most intensively farmed and most consumed mammal in Europe (FAO Stats, 2017). Previously (section 1.2 from page 5), I explained why a better understanding of personality and affective states is a necessary step to improve animal welfare and both topics have already been well studied in pigs (Murphy et al., 2014; O'Malley et al., 2019). Indeed, there are an increasing number of studies that investigate pigs' affective states with established methods and that show the advantage of using the componential view of emotions (presented in section 1.2.2 from page 8). Those studies combine the measurements of behavioural reactions with cognitive (Düpjan et al., 2017), autonomic (Imfeld-Mueller et al., 2011; Krause et al., 2017; Zebunke et al., 2011), bioacoustic (Friel et al., 2019; Leliveld et al., 2016) or facial (Camerlink et al., 2018b) reactions. Thus, pigs represent a good model to investigate the mechanisms of emotional valence. Additionally, personality of pigs has been also well explored, especially coping determined with the *Backtest* (Hessing et al., 1993; Jensen et al., 1995; Zebunke et al., 2017; Zebunke et al., 2015), but also various personality traits determined with the use of the *Open-Field*, *Novel Object*, *Human Approach* or *Open Door Tests* (reviewed in O'Malley et al., 2019).

Since the focus of this thesis is to explore the potential of studying behavioural lateralization to help improve animal welfare, it seems that pigs represent an ideal model. In this species, there are indications of cerebral (van der Beek et al., 2004), behavioural (Camerlink et al., 2018a; Gill & Thomson, 1956; Illmann et al., 2002; Newberry & Wood-Gush, 1984) or physiological (Telkänranta et al., 2016) asymmetries. However, no theory-driven studies have been yet conducted on behavioural lateralization in this species although it should be helpful for pig welfare. As omnivorous ungulates, pigs have well-developed motor skills, especially with their snout since they use it for rooting (D'Eath & Turner, 2009), for washing food (Sommer et al., 2016), and potentially for using tools (Root-Bernstein et al., 2019). Thus, one might expect them to show individual lateralized motor patterns for their snout at least, since this function seems similar to the hand of primates (see section 1.3.3 from page 18). Concerning their visual system, they show a wide monocular field with a strong decussation of their optic fibres (Herron et al., 1978; Hughes, 1977) suggesting that most visual inputs of an eye are processed by the contralateral hemisphere. This has been validated by brain imaging studies on the visual cortex of pigs (Fang et al., 2006; Gizewski et al., 2007). Thus, this species seems to fulfil the prerequisite to use motor and visual lateralization to gain insight into pig's personality and emotions.

1.5 Hypotheses and aims of the thesis

1.5.1 General aim of the thesis

This thesis aims at exploring how studying laterality in pigs might help improve animal welfare through providing insight into their personality and their emotions (see Figure 1.3 on page 31 which summarizes the aims of this thesis). The previous sections showed that this approach has the potential to non-invasively expand our understanding of the neural roots of emotions and of some personality traits. Indeed, since research on both personality and emotions is needed to improve farm animal welfare (explained in section 1.2 from page 5), the domestic pig seems to be an ideal model for investigating motor and visual laterality (explained in previous section) in order to test hypotheses on emotional lateralization (explained in section 1.3 from page 14). Thus, this work represents the first theory-driven studies on behavioural lateralization in pigs with potential implications for welfare. This thesis is organized according to two main questions that were explored with three studies (see Figure 1.3):

- Is individual hemispheric dominance measurable through individual lateralized motor patterns and does it reflect personality in pigs?
  - Can the observation of individual motor biases be indicative of hemispheric dominance? (Study 1)
  - Are individual differences in motor biases of pigs associated with their personality? (Study 2)
- Can the direct investigation of emotional lateralization in pigs improve understanding of the mechanisms of emotional valence?
  - Does the manipulation of visual information processing (through monocular viewing) in pigs influence their reaction towards stimuli of different valences? (Study 3)

1.5.2 Experimental approach

To answer these questions we used different methodological approaches for each study which are also summarized in Figure 1.3. In the first study, we investigated laterality of several motor functions, since this allows accounting for the multidimensionality of laterality (explained in 1.3.3 from page 18). This aimed at providing the first comprehensive overview in pigs on how several motor functions (involving their snout, foot and tail) differ in their lateralization patterns. Pigs are trainable animals (reviewed by Gieling et al., 2011) which makes this species suitable to investigate lateralization for different motor tasks such as using their snout for reaching food. In this study, we could explore how stable individual motor lateralization patterns are, which required multiple measurements per individual over several days. As generally recommended in the literature (Branson & Rogers, 2006; Leliveld, 2019; Tomkins et al., 2010a), we calculated the laterality indices and the binomial z-scores (see the methods section of Study 1 from page 38) of each individual for each motor function in order to describe how the motor lateralization patterns differed between motor functions and individuals. After this step, we combined laterality

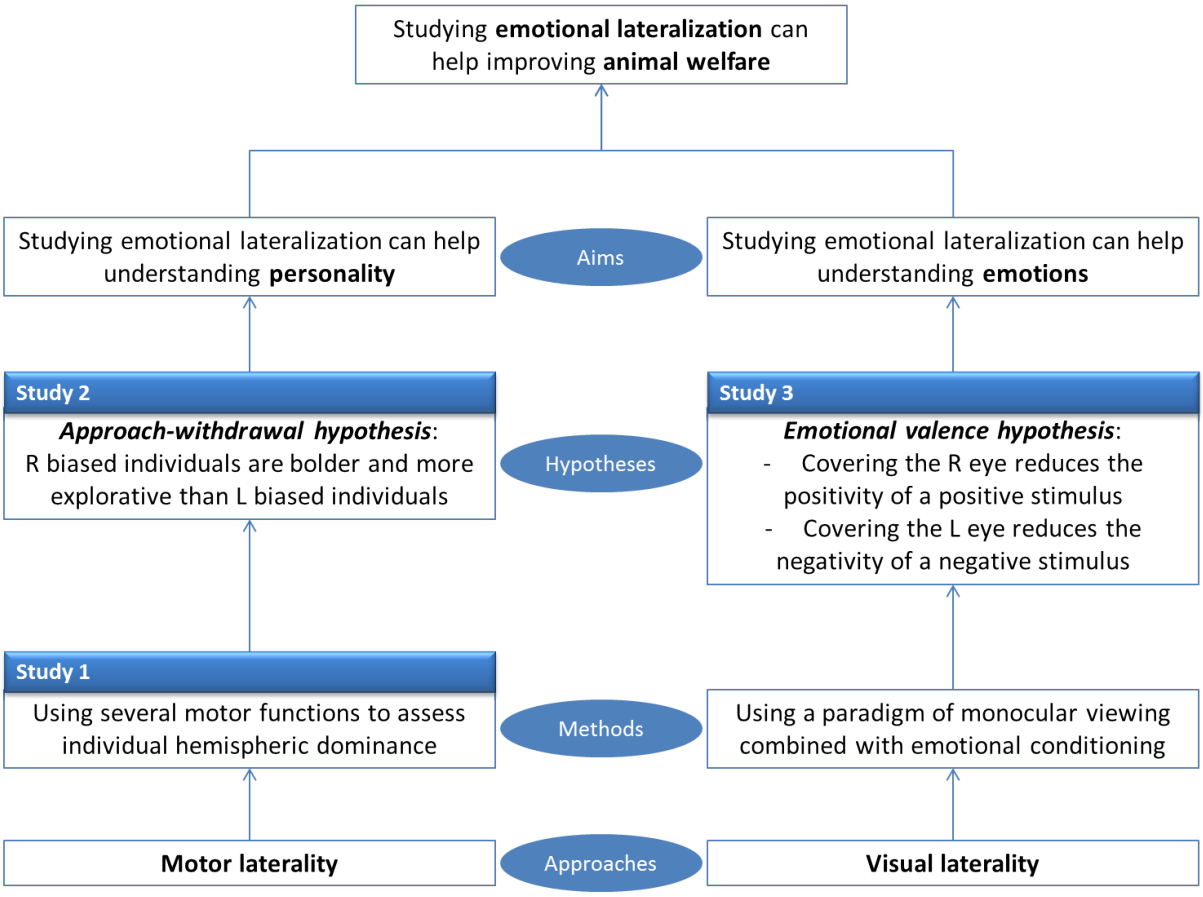

Figure 1.3: *Summarized aims and hypotheses of the thesis showing the methodological approaches used according to each study*

indices of several motor functions in order to classify individuals with consistent motor biases across motor functions, using a cluster analysis. Those individuals in particular were supposed to have a clear individual hemispheric dominance that has been used in the second study.

In the second study, we compared the pigs with L vs. R consistent motor biases (with supposed opposite individual hemispheric dominances, determined by the cluster analysis in the first study) along several personality dimensions (according to the five dimensional model of Réale et al., 2007), as recommended by several authors (Finkemeier et al., 2018; O'Malley et al., 2019). It is important to clarify that we tested the pigs only once, since the first exposure to a test can be considered as an appropriate indication of personality in pigs (Forkman et al., 2007; O'Malley et al., 2019). To achieve this, we used several established personality tests in pigs that give insight into several personality traits: the *Backtest*, the *Human Approach Test*, the *Open Door Test*, the *Open-Field Test* and the *Novel Object Test*. As recommended by O'Malley et al. (2019), we assigned each parameter of each personality test to a specific personality trait (e.g. the latencies to touch the novel human, to touch the novel object and to leave a familiar environment gave insight into boldness; for a comprehensive description, see the methods section of Study 2, from page 55). We also measured their basal cortisol and testosterone concentrations since it might also be associated with some personality traits, such as boldness or aggressiveness.

In the third study, we studied emotional reactions by using a monocular viewing paradigm

while measuring behavioural reactions and responses of the autonomic nervous system (through heart rate variability measurements). Aside from accounting for the componential view of emotions (Paul et al., 2005), we combined indicators of emotions from the CNS and the PNS, as recommended by Hagemann et al. (2003). Indeed, as highlighted in section 1.3.5 from page 24, monocular viewing (achieved through eye patching) can be considered as a direct manipulation of the CNS in pigs during emotional processing, and is the most insightful method to directly control which hemisphere gets inputs (Rogers, 2017b). As pigs are easy to handle, the method of eye patching seems ideal to test visual laterality in this species (Rogers, 2017b). This could represent a valuable addition to research on emotional valence in farm animals since only a few studies have used the paradigm of monocular presentation in the context of emotional processing. Moreover, we used a paradigm of emotional conditioning (i.e. the pigs associated an artificial object with a negative or positive stimulus) which would guarantee a predominant focus on emotional valence (explained in section 1.3.5).

1.5.3 Study-specific hypotheses

Figure 1.4 (page 33) illustrates the details of each hypothesis tested in the studies of this thesis. The first study aimed at finding indications of pigs' individual hemispheric dominance. We first aimed at combining several motor lateralization patterns. After this step, we hypothesized that there would be individuals with consistent and stable lateralization patterns across motor functions, revealing the existence of individual hemispheric dominance in pigs (see Figure 1.4).

The second study aimed at linking pig's personality with the individual hemispheric dominance determined in the first study and to find out whether the results are in line with the approach-withdrawal hypothesis. As illustrated in Figure 1.4, we hypothesized that pigs with a L individual hemispheric dominance (expressed through R consistent biases across motor functions) are bolder and more explorative than pigs with a R individual hemispheric dominance (expressed through L consistent biases across motor functions). This study aimed at answering the question of whether using motor laterality might be helpful for research on pig personality (see Figure 1.3, page 31).

The third study aimed at directly testing the emotional valence hypothesis in pigs (see Figure 1.4). In contrast to the other studies, the lateralized processing of emotions at the population level was directly investigated. We expected that the emotional reaction towards a valenced stimulus would be modified along the emotional valence axis according to which eye sees it. In particular, we hypothesized that reducing inputs into the L hemisphere (achieved through covering the R eye) would reduce the positive appraisal of a positive stimulus while reducing inputs into the R hemisphere (achieved through covering the L eye) would reduce the negative appraisal of a negative stimulus. Thus, this study should give insight into how using visual laterality may complement the componential view of emotions and may improve the understanding of their mechanisms in pigs (see Figure 1.3).

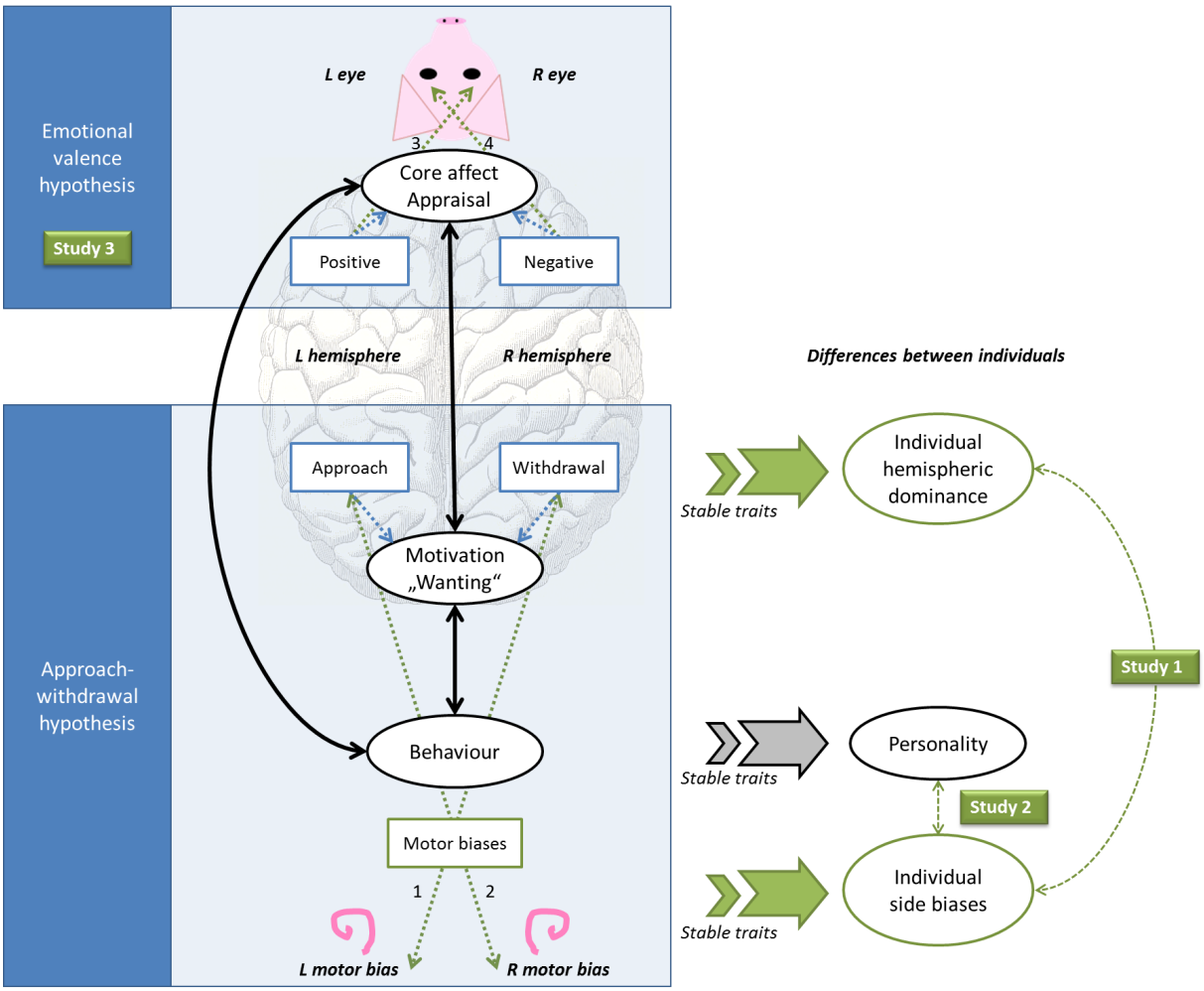

Figure 1.4: *Representation of the investigated hypotheses on emotional lateralization according to each study (in green) combined with Figure 1.2, page 17*

Solid lines represent the links between the core concepts of this thesis (in oval shapes), presented in Figure 1.1, page 13. Big right pointing arrows illustrate that stable traits in e.g. behaviour or affect result in the emergence of personality or affective styles (explained in Figure 1.1). Blue dotted lines link the predictions of each hypothesis (in rectangular shapes) to each proposed core concepts of this thesis (explained in Figure 1.2). Green dotted lines show which links the studies aimed at testing. Green double directed lines reflect that associations were tested while green one-directed lines reflect that causal links were tested. In Study 1, we assessed motor biases in pigs (with the example of tail curling in this illustration) and assumed that consistent individual biases (see the big right pointing arrow) would reflect individual hemispheric dominance (i.e. the preferred use of the left (L) or the right (R) hemisphere in general). This concept of individual hemispheric dominance might represent an alternative to measurements of cerebral baseline asymmetries used in affective styles research (explained in section 1.3.4, from page 20). In Study 2, we aimed at studying the associations between personality and individual side biases. Using the approach-withdrawal hypothesis, we expected that L motor biases would be associated with withdrawal behaviours (1) while R motor biases would be associated with approach behaviours (2). In Study 3, we investigated how the manipulation of visual inputs coming into the L or the R hemisphere influenced emotional reactions. Using the emotional valence hypothesis, we expected that covering the R eye would reduce positive appraisal (3) while covering the L eye would reduce negative appraisal (4).

"The creatures outside looked from pig to man, and from man to pig, and from pig to man again; but already it was impossible to say which was which."

George Orwell (1903-1950), Animal Farm

2

Experimental Studies

2.1 First Study: Behavioural lateralization in domestic pigs (*Sus scrofa*)

— Variations between motor functions and individuals

Charlotte Goursot[a], Sandra Düpjan[a], Armin Tuchscherer[b], Birger Puppe[a,c], Lisette M. C. Leliveld[a]*

[a]Institute of Behavioural Physiology, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,
[b]Institute of Genetics and Biometry, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,
[c]Behavioural Sciences, Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany

*Contact: Lisette M. C. Leliveld: leliveld@fbn-dummerstorf.de

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Abstract

Motor lateralization is hypothesized to depend on the complexity of the motor function, but it might at the same time reflect hemispheric dominance within an individual across motor functions. We investigated possible motor lateralization patterns in four motor functions of different complexity (snout use in a manipulative task, foot use in two-stepping tasks and tail curling) in the domestic pig, a tetrapod species relevant as farm animal but also as a model in human neuroscience. A significant majority of our sample showed individual biases for manipulation with their snout and for curling their tail. Interestingly, the tail curling was lateralized towards the right at the population level and showed stronger lateralization patterns than the snout. Using a cluster analysis with combined tail and snout laterality, we identified groups of individuals with different lateralization patterns across motor functions that potentially reflect the individuals' hemispheric dominance. To conclude, our results suggest that pigs show lateralization patterns that depend on the motor function and on the individual. Such individual lateralization patterns might have broader implications for animal personality and welfare. Our study lays the methodological groundwork for future research on laterality in pigs.

Keywords

task complexity; motor lateralization; foot; snout; tail curling

2.1.1 Introduction

Cerebral asymmetries are widespread in animals and are supposed to have an evolutionary advantage to improve brain efficiency by enabling the brain to perform more than one task simultaneously (Rogers et al., 2004). These asymmetries are observable through behavioural lateralization, e.g., motor lateralization, which is expressed behaviourally through side biases. The best-studied example of motor lateralization is handedness in humans, with the majority of the human population being strongly lateralized at the individual level (individuals have a strong preference to use one hand over the other; Oldfield, 1971), and a population-wide bias towards the right (the majority is right handed; Annett, 1985; Corballis, 2009). A number of studies show that motor lateralization is common in non-human vertebrates (Frasnelli, 2013; Rogers et al., 2013; Ströckens et al., 2013) and even in invertebrates (Frasnelli, 2013), but findings are often disparate (Ströckens et al., 2013; Versace & Vallortigara, 2015).

The sometimes contradicting findings may be partially explained by the fact that different studies focus on different motor functions. According to the "task complexity hypothesis", more complex tasks elicit stronger lateral biases on the individual level and are more likely to elicit population-level biases (Fagot & Vauclair, 1991). For example, in many primate species bimanual coordinated tasks, in contrast to simple (unimanual) tasks, elicit stronger hand preferences (reviewed by Hopkins, 2013) and sometimes a population bias (Molesti et al., 2016). However, many species do not use their limbs for tasks of different complexity, such as walking and grabbing, which limits the testing of limb use in a variety of tasks. For this reason, some authors adapted the "task complexity hypothesis" into the "organ complexity hypothesis" (Keerthipriya et al., 2015), which suggests that the strength of lateralization varies between different organs. Specifically, unpaired organs are suggested to be more complex than paired organs. For example, in food-reaching tasks, elephants are more strongly lateralized in the use of their trunk than their forefeet (Keerthipriya et al., 2015) and spider monkeys are more strongly lateralized in the use of their tail than their hands (Laska, 1998). From these conclusions, one can deduce that laterality varies across task and/or organ complexity. In this article, we will refer to these combined effects as "motor function complexity". To get an overview of motor lateralization in a certain species, studies should ideally include different motor functions.

While the strength of lateralization can be influenced by the complexity of the task, we might also find consistent lateralization patterns within an individual, and variation between individuals. Indeed, "each individual has a tendency to use either its left or right hemisphere predominantly" (Rogers, 2009), which is assumed to be observable through individually consistent lateral preferences (Wright & Hardie, 2015). In this article, we used the term "individual hemispheric dominance" to describe this phenomenon. Many studies have found interactions between individual motor lateralization patterns and other individually distinct behavioural patterns, such as anxiety (Branson & Rogers, 2006; Hicks & Pellegrini, 1978; Wright & Hardie, 2012) or approach/avoidance behaviours (Hardie & Wright, 2014; Hopkins & Bennett, 1994; Watson & Ward, 1996), as a consequence of this individual hemispheric dominance. Thus, studying motor lateralization patterns on the individual level represents a promising approach in the study of personality, i.e., consistent individual behavioural differences over time and/or across situations (Réale et al., 2007). Since personality plays an important role in an individual's response

to environmental challenges and therefore its welfare, the study of (motor) laterality could contribute to animal welfare research (Leliveld et al., 2013; Rogers, 2010, 2011).

As the domestic pig (*Sus scrofa*) is one of the most intensively farmed species in the world and is progressively used as a model in human neuroscience (Kornum & Knudsen, 2011; Lind et al., 2007; Sauleau et al., 2009), it is important to know more about lateralization in this species. Apart from some indications on cerebral asymmetries (van der Beek et al., 2004), and some reports on side preferences during nursing in lactating sows (Gill & Thomson, 1956; Illmann et al., 2002; Newberry & Wood-Gush, 1984), lateralization was never systematically studied in this species before.

Our study aim was to provide a first comprehensive overview of motor lateralization in the domestic pig. Thereby, we explored motor lateralization in three different organs: snout, foot and tail. We tested the snout use in a manipulative task, foot use was tested in two stepping tasks, and we observed the direction during the spontaneous curling of the tail.

Pigs search for food, using their snout to explore, collect, carry, manipulate and even wash food items (Gundlach, 1968; Sommer et al., 2016; Stolba & Wood-Gush, 1989). Therefore, the pig snout seems to fulfil similar functions as the hands of primates or the trunks of elephants, making it suitable for studying motor lateralization. As even-toed ungulates (Artiodactyla), their foot use represents another important motor function. A third interesting and easily observable motor function of the pig is the curling of the tail. Tail curling behaviour was found to occur more often during interactions with a familiar person (Kleinbeck & McGlone, 1993), while other authors (Reimert et al., 2013) recently found that this behaviour occurs in more neutral emotional contexts, in comparison to tail wagging (more in positive contexts) or tail hanging (more in negative contexts).

The "motor function complexity hypothesis" suggests that the snout, being the most complex function (an unpaired organ performing a manipulative task), would show the strongest lateralization patterns, while the feet (as paired organs performing a simple stepping task) would show the weakest lateralization patterns. In addition, we expected to find individual lateralization patterns across motor functions (as an indication of an individual's hemispheric dominance), when all motor lateralization patterns were combined.

2.1.2 Materials and methods

Ethical note

The experimental procedure was approved by the ethics committee of the federal state of Mecklenburg-Western Pomerania, Germany (LALLF M-V/TSD/77221.3-2-040/14-1).

Animals and housing

The study was conducted at the Experimental Facility for Pigs of the Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany. The subjects were 80 (among 100 pre-selected; see below) pre-pubertal, uncastrated male German Landrace piglets (aged 5–7 weeks during the experimental period). Experiments were performed with five consecutive replicates between November 2014 and May 2015. As a standard procedure of the Experimental Facility for Pigs,

within the first 24 hours after birth, the tip of the tail (maximal length of 1 cm) was routinely clipped off. Before weaning, the subjects were submitted to 4 *Backtests* (at the age of 5, 12, 19 and 26 days) to determine their coping style, using the standardized method of Zebunke et al. (2015). At 4 weeks of age, 20 individuals were pre-selected from a greater pool based on their health status, absence of injuries (including a tail without injuries), weight (greater than 5 kg), and their coping style (preferring active and passive over doubtful/intermediate coping styles; these results will be discussed in another publication). The number of full siblings was set to a maximum of 4 for preselection.

The pre-selected pigs were weaned (day 0) and grouped together in a pen (3.75 x 1.8 m, with fully slatted plastic floors and a solid heated area in the middle), where they had access to food and water ad libitum. From days 3–5 post-weaning, the pigs were habituated to being handled by the experimenter (2 sessions of 1 hour per day) who distributed during each session two handfuls of chocolate raisins in the pen in order to habituate the pigs to the food reward. Chocolate raisins are common rewards used in pig behavioural studies (Gieling et al., 2011). On day 6, each pig was guided to the corridor that was adjacent to the pen and stayed there, physically isolated from the group for a maximum of 10 minutes. During this time, 5 chocolate raisins were thrown on the floor of the corridor, and each individual was assessed on its motivation to eat when alone (varying from 1 to all raisins eaten). For the experiment, we selected 16 individuals using the following criteria (in order of importance): the absence of illness/injuries, eating the reward alone, active or passive coping style, relatedness to other subjects (avoidance of full siblings where possible) and the absence of nervousness. Each subject was randomly given an ID-number, which determined the test order throughout the entire experiment. At the end of the last handling day (day 6), the 20 pigs were moved into a new pen (2.50 x 3.95 m) with fully slatted plastic floors and two solid concrete sections. This pen was in the same room as the experimental arena (see below for the setup description). During the experimental period, the subjects were fed an age-appropriate ration once per day after the last session of the day. This setup was used to ensure standardized motivation among subjects for performing the food-retrieval test. Water was available ad libitum, and straw and some other physical enrichments (buckets, rags, etc.) were provided twice a day during the entire experimental period.

Snout and foot use

Experimental setup

Lateralized manipulation with the snout and foot use were tested in a symmetrical arena (1.5 x 1.5 m, see Figure 2.1). This arena was connected to the home pen through a corridor (51 x 185 cm) that was used as a waiting area (between trials). A sliding guillotine door (39 x 45 cm) that could be operated from the corridor was used to provide access to the arena. A ramp was placed at the end of the corridor, creating a 6.5-cm high step into the arena. In the arena, on the opposite side of the sliding door, a flap door (22 x 30 cm) was integrated in the middle of the wall (105 cm high). Behind this flap door, a trough (5 cm high) containing a food reward (one chocolate raisin) was positioned. A fixed tube was used to ensure that the raisin was always positioned in the middle of the trough. After the 6 training sessions (18 trials), the setup

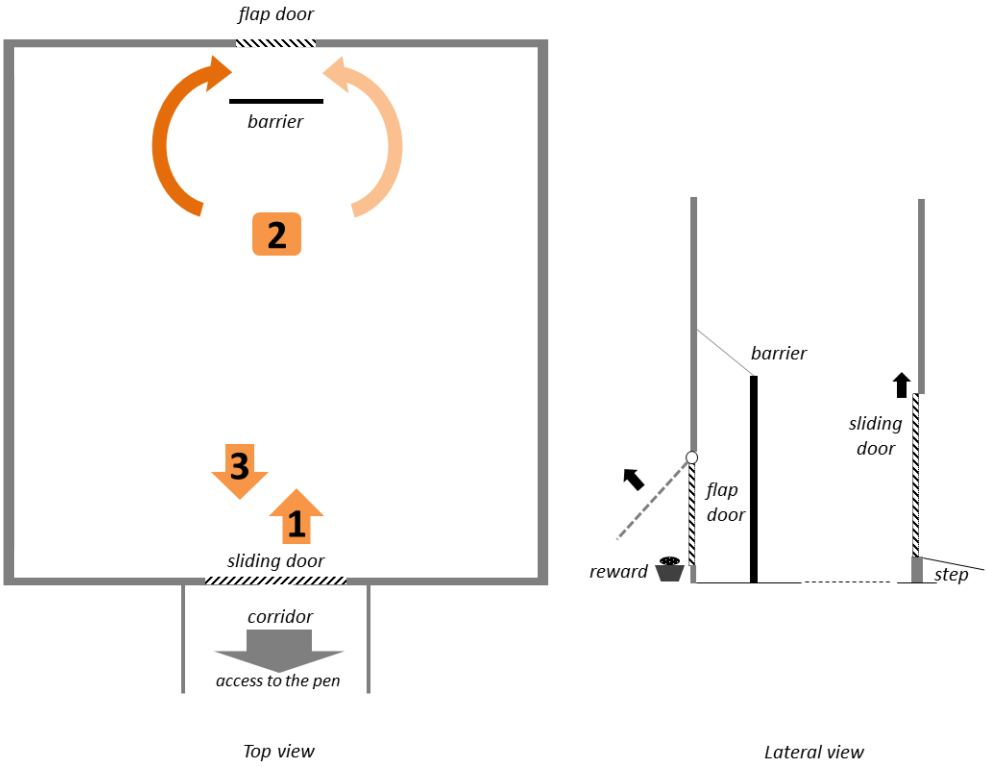

Figure 2.1: Schema of the testing arena.

The curved arrows at the top indicate how the subject may have opened the flap door in each case. The pale arrow indicates that they opened the flap door with the right side of the snout, and the dark arrow indicates that they opened the door with the left side of the snout. The numbers describe the testing procedure per trial: 1. Foot down; 2. Manipulation with the snout to open the flap door; 3. Foot-up.

was modified for the test situation: a fixed barrier (26 x 57 cm) was placed 15 cm in front of the flap door, so that the subjects were forced to approach the flap door from the side and then use the left or right side of the snout to open it.

A camera was positioned on the wall above the flap door and was focused on the entrance of the sliding door. Another camera, connected to a digital video recorder, was positioned centrally above the arena.

Experimental procedure

The experimental period consisted of 10 working days. The training period began on day 8 and consisted of 6 sessions across 4 working days (2 sessions per day on days 8 and 11 and 1 session per day on days 12 and 13). The test period began on day 13 (after the last training session) and consisted of 10 sessions across 7 working days (2 sessions per day on days 14, 15 and 18 and 1 session per day on day 13 and days 19 through 21). In total, each pig performed a maximum of 30 trials. Morning sessions were performed between 08:00 and 10:00 and afternoon sessions between 11:30 and 14:00.

To improve the training's efficiency by using social facilitation, the first three sessions were performed with randomly paired pigs. New pairs were formed for each session so that each

subject could learn to access the reward in a short amount of time. The last three training sessions were performed with the subject alone; this was done to habituate the pigs to the testing procedure, which was also performed alone. The barrier (before it was fixed in the arena) was presented in the home pen for 10 minutes once per day during the last three training days, so that the subjects were habituated to it before the start of the test sessions.

Before each session, the experimenter entered the pen and gently guided a subject into the corridor. The subject was then offered a chocolate raisin while waiting in the corridor. Each trial consisted of the following procedure (see the video in the supplemental data): The experimenter pulled up the sliding door and the subject entered the arena. When a subject successfully opened the flap door and retrieved the chocolate raisin, the sliding door was re-opened. In the corridor, the subject received another chocolate raisin. The experimenter put a new raisin in the trough. If the raisin was still there, the measurement for snout use was counted as "failed". Since only 0.03% of all trials were counted as failed, these trials were not included in the analysis. Per session, this procedure was repeated 3 times (i.e., for a total of 3 trials). A session finished after the third successful retrieval of the food reward, or when a maximum of 10 minutes had passed. At the end of the session, the experimenter opened the door connecting the corridor to the pen, so that the subject could return to the pen. Between subjects, the experimenter cleaned the floor of the arena as well as the barrier and flap door.

Tail curling direction

The tails were observed before and after each experimental session (6 training + 10 test sessions). A total of 32 observations per subject were made. The observations were done in the following way: The experimenter entered the pen, provided either fresh straw or some toys (rags, shoes) to the pigs and noted the curling direction from pigs that were either standing or walking. The order of observations was determined by the behaviour of the pigs: The moment a pig with a curled tail was spotted, the direction was noted down.

Three observations were possible (Figure 2.2): left curling (L; the tip of the tail is situated to the left of the base), right curling (R; the tip of the tail is situated to the right of the base) or an "unclear" curling (mostly curling in the middle; the tip of the tail showed no clear deviation from the middle). Observations of "unclear" curling were excluded from further analyses.

Behavioural analyses

Observations of snout and foot use were performed using video recordings by the same observer. As the subject entered the arena, the front foot that entered the arena first was observed (Figure 2.1: "1. Foot down"). When a subject successfully opened the flap door and retrieved the chocolate raisin, the side of the snout used was observed (Figure 2.1: "2. Snout use"). As the subject exited the arena, the front foot that entered the corridor first was observed (Figure 2.1: "3. Foot-up"). To ensure the reliability of the video observations, we compared a sample of observations from one randomly selected replicate (2 test sessions, 96 trials) with a second observer and obtained the following Kappa coefficients: 0.92 for the snout, 0.81 for foot down and 0.82 for foot-up, which indicated almost perfect agreement.

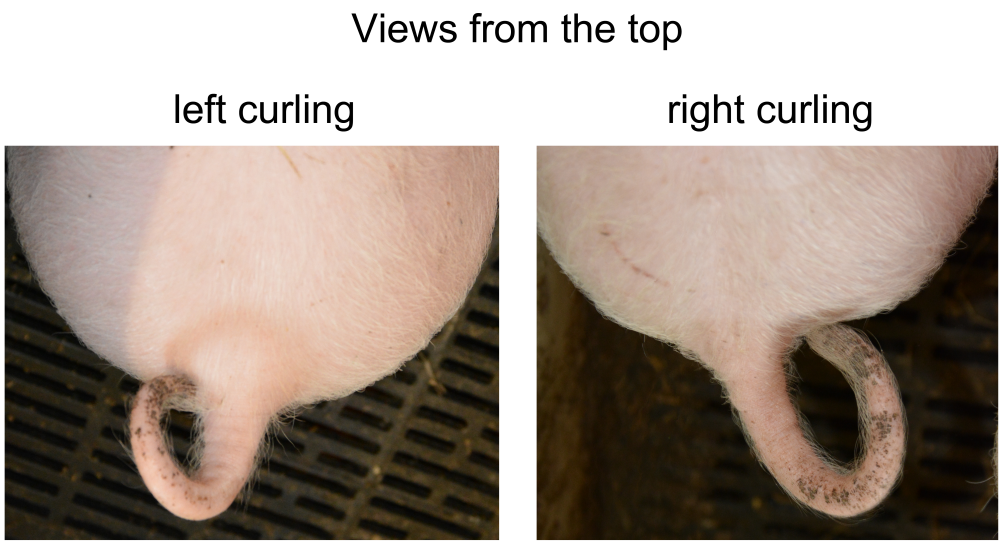

Figure 2.2: Examples of clear tail curling directions.

Statistical analyses

We used SAS version 9.4 (SAS Institute Inc., Cary, NC, USA) for our statistical analyses. To determine if an individual had a significant bias for one side over the other, we used a simplified binomial test. For this, we calculated an individual z-score (Branson & Rogers, 2006) using the formula:

$$z = \frac{R - (R+L)/2}{\sqrt{(R+L)/4}},$$

where R is the number of right choices and L is the number of left choices. A z-score≤−1.96 indicates a left bias (L), a z-score≥1.96 indicates a right bias (R), and a value between these two scores indicates no lateral bias (i.e., ambilateral; A). Using a chi-square test (FREQ procedure), we determined if a significant majority of the subjects were lateralized. To test this, we compared the number of L- and R-individuals with the number of A-individuals (H0: distributions R + L= 50%; A = 50%). If there were significantly more lateralized individuals, we also compared the number of R-individuals with the number of L-individuals (H0: R = 50%, L = 50%). If we found a significant difference between the amount of L- vs. R-individuals, we finally determined if our tested population had a significant bias for the left or the right for each motor function (i.e., for an R population bias, H0: R = 50%, L + A = 50%). In addition, we also calculated a continuous laterality index (LI; adapted from Hopkins, 1999) for each subject and motor function by using the formula:

$$LI = \frac{R - L}{R + L},$$

where R is the number of right observations and L is the number of left observations. This index ranges from −1 to 1, with positive values reflecting a right bias and negative values a left bias. The absolute value of LI (LI_ABS) was used to indicate the strength of laterality. In this case, the index ranged from 0 to 1, with low values reflecting a weak bias and high values reflecting a strong bias. To provide a graphical representation of distribution across these indices, we used JMP 12.0.1

(SAS Institute Inc., Cary, NC, USA). We transformed our distribution data into a smoothed curve, using a Kernel standard deviation of 0.1063. This smoothed curve was then visually compared to different adapted distribution models (normal or a mixture of several normal distributions) to determine the type of distribution.

We tested for trial effects by comparing the number of L vs. R choices for snout use between the beginning (trials 1–14) and the end (trials 15–30) of the testing. Using the MIXED procedure, an analysis of variance (ANOVA) was calculated with the percentage of choices (L or R) as a variable and the phase of testing (beginning or end) as a fixed factor. We also compared the strength of lateralization between the different motor functions using the MIXED procedure; an ANOVA was calculated with LI_ABS as a variable and the motor function as a fixed factor. Multiple pairwise comparisons were calculated using Tukey-Kramer tests. To control for the effect of replicates, we performed the same ANOVA with the LI and the LI_ABS as variables and the replicate as a fixed factor.

A chi-square (FREQ procedure) test was performed to test for associations between the different motor functions. To detect individual lateralization patterns across motor functions, we used a cluster analysis to obtain a combined laterality classification. For this analysis, we selected the LIs of motor functions that followed a bimodal distribution. These LIs were first standardized using the STDIZE procedure. Next, we performed the FASTCLUS procedure (maxiter = 100, strict = 0.9, nomiss). STRICT prevents an observation from being assigned to a cluster if its distance to the nearest cluster seed exceeds the value assigned to the STRICT variable. We tested for 2, 3, 4 and 5 clusters (i.e., maxcluster =2, 3, 4 and 5) to determine the number of clusters that best represented the variation in the data. The reliability of the model is given by the cubic clustering criterion (CCC values greater than 2 or 3 indicate good clusters) combined with a graphical verification. For a continuous representation of the combined laterality, we calculated a combined LI for each individual, based on the mean of the laterality indices that were included in the cluster analysis. A graphical representation of the distribution across this index was created in JMP 12.0.1 (SAS Institute Inc., Cary, NC, USA).

2.1.3 Results

For technical reasons, we could not observe the foot use during the first replicate (n = 16). During the food-retrieval test, all subjects learned to open the flap door, but four subjects were excluded from the snout and foot-use analyses because they could not learn to eat the reward alone. Two other subjects were excluded from the tail analyses because the number of R and L observations was not sufficient to perform the individual binomial tests. This resulted in the following sample sizes per motor function: n = 76 for snout, n = 60 for foot-up and foot down and n = 78 for tail curling.

There was no effect of the test phase (beginning vs. end) on the percentage of R or L choices for snout use, $F(2, 211.1) = 0.3$, $p = .74$. We found a significant effect of the replicate on the strength of snout laterality, $F(4, 71) = 5.7$, $p < .001$. The pairwise comparisons revealed that the second replicate showed significantly weaker snout laterality compared to the fourth, $t(71) = -3.78$, $p < .01$, and the last, $t(71) = -3.39$, $p < .01$, replicates, while the third replicate showed significantly weaker snout laterality compared to the fourth replicate, $t(71) = -3.13$, $p < .05$.

Lateralization patterns by motor function

Table 2.1 and Figure 2.3 show the distributions for all motor functions across the different laterality categories and indices, respectively. For snout, significantly more individuals were lateralized than not lateralized, $\chi^2 = 278.421$, $DF = 1$, $p < .001$, $n = 76$. The number of individuals with a bias for the right side of the snout did not differ significantly from the number of individuals with a bias for the left side, $\chi^2 = 0.1475$, $DF = 1$, $p = .7009$, $n = 61$. Figure 2.3 shows the distribution of the tested population for the snout LI. The smooth curve plotted by JMP was found to resemble an adapted mixture of two normal distributions, with two peaks at the extremes (at $LI = -1$ and $LI = 1$).

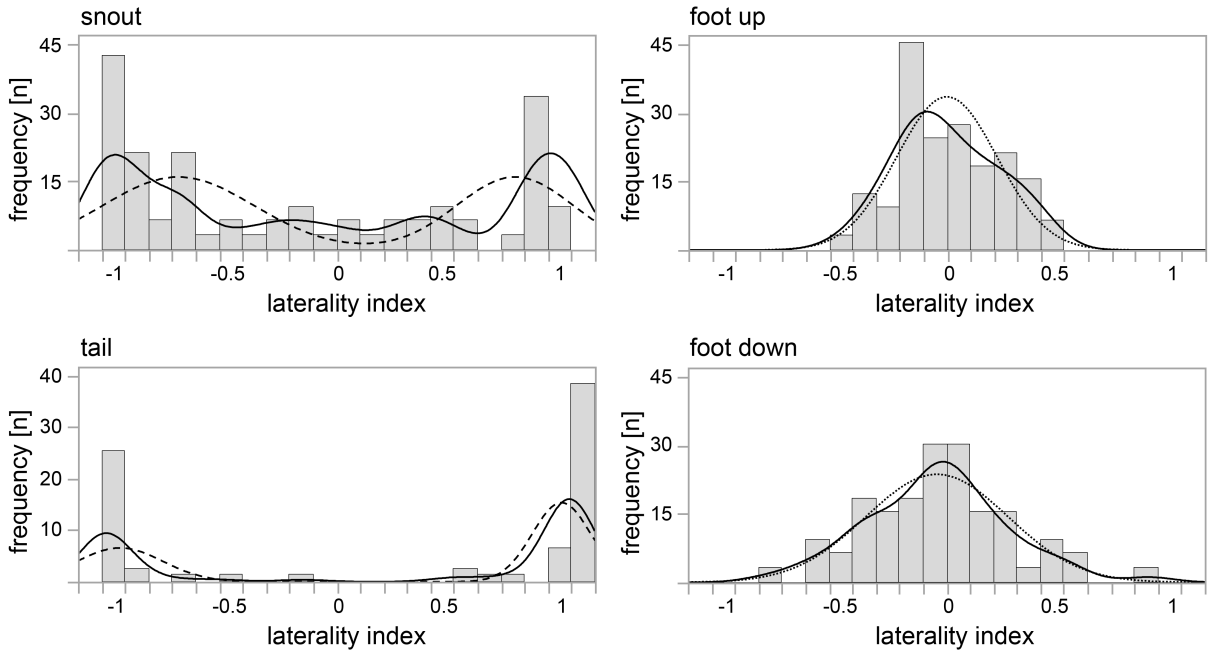

Figure 2.3: Distribution of the individuals according to their laterality indices (with an increment of 0.1).

Positive values reflect a right bias and negative values a left bias. Solid lines indicate the smooth curve that is plotted in JMP. Dashed lines indicate the calculated mixture of two normal functions, and dotted lines indicate the calculated approximation of a normal function.

Significantly more individuals were ambilateral than lateralized for stepping down, or into, and stepping up, or out of, the experimental arena (foot down: $\chi^2 = 416.667$, $DF = 1$, $p < .001$, $n = 60$; foot-up: $\chi^2 = 192.667$, $DF = 1$, $p < .001$, $n = 60$). Figure 2.3 shows the distribution of the foot laterality indices. The smooth curves plotted by JMP were found to resemble a normal distribution, with one peak at $LI = 0$.

For tail curling, significantly more individuals were lateralized than not lateralized, $\chi^2 = 702.051$, $DF = 1$, $p < .001$, $n = 78$. There were significantly more individuals with a right bias for tail curling than individuals with a left bias, $\chi^2 = 52.632$, $DF = 1$, $p = .0218$, $n = 76$. There were also significantly more right-biased individuals compared to non-right-biased individuals (L + A subjects), which indicates a population-level right bias for the tail curling direction, $\chi^2 = 41.538$, $DF = 1$, $p = .0415$, $n = 78$. Figure 2.3 shows the distribution of the tested population for the tail

LI. The smooth curve plotted by JMP was found to resemble an adapted mixture of two normal distributions, with a high peak at $LI = 1$ (right) and a somewhat lower peak at $LI = -1$ (left).

Table 2.1: The number of subjects per laterality category for each motor function (based on the binomial test).

Motor function	R	L	R + L	A
Snout	29	32	61	15
Foot-up	6	7	13	47
Foot down	4	1	5	55
Tail	48	28	76	2

Note: R = individuals with a significant right bias, L = individuals with a significant left bias, R + L = lateralized individuals, A = ambilateral individuals without a significant bias.

The comparison of the LI_ABS between the different motor functions is shown in Figure 2.4. The motor function had an effect on the strength of laterality, $F(3, 71.6) = 408.5$, $p < .001$. The pairwise comparisons revealed that the LI_ABS for tail was significantly the highest (compared to snout: $t(76.7) = -6.05$; foot down: $t(78.0) = -32.0$; foot-up: $t(71.5) = -23.5$; all $p < .001$). The LI_ABS for snout was still higher than the LI_ABS for both foot functions (foot down: $t(74.8) = -14.0$; foot-up: $t(72.2) = -12.4$; all $p < .001$).

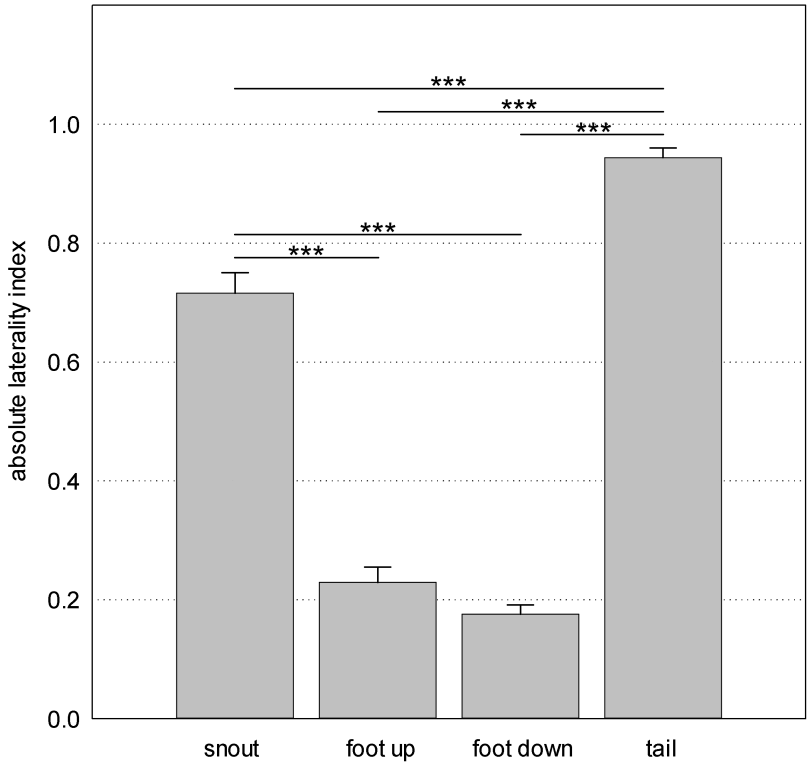

Figure 2.4: Absolute values of the laterality indices for the different motor functions (least square means and standard errors).

Table 2.2: The number of subjects per combined tail and snout bias (based on the binomial test).

Motor function	Snout		
Tail	R	L	A
R	16	21	9
L	12	10	4
A	0	1	1

Note: R = individuals with a significant right bias, L = individuals with a significant left bias, A = ambilateral individuals without a significant bias.

Individual lateralization patterns across motor functions

The LI for snout use and tail curling showed a bimodal distribution, while the LI for the two-foot functions showed a normal distribution; thus, we only included the LIs of snout and tail curling in the analysis of a combined laterality classification. The snout side categories were not significantly associated with the tail curling direction categories (χ^2 = 2.7688, DF = 4, p = .597228, n = 74; see Table 2.2).

Using the FASTCLUS procedure, we obtained 4 reliable clusters (CCC = 14.17, n = 74; Figure 2.5). We could distinguish four main clusters located in the four quadrants of the two-dimensional space that is created by the snout and tail LIs. As seen in the graphical representation (Figure 2.5), there were 18 right-biased (for both functions) subjects in the RR cluster, 12 left-biased (for both functions) subjects in the LL cluster, 15 subjects in the RL cluster (right biased for snout use and left biased for tail curling), and 25 subjects in the LR cluster (right biased for tail curling and left biased for snout use). Based on the STRICT criterion (0.9), four individuals were not assigned to any of these clusters. Note that the classification based on cluster analysis can deviate from the classification based on the binomial tests.

Figure 2.6 shows the distribution of the tested population for the combined LI, which is the mean of the laterality indices of both lateralized motor functions (tail and snout). The smooth curve was found to resemble an adapted mixture of three normal distributions, with two peaks at the extremes (at LI = −1 and LI = 1) and one peak in the middle (at LI = 0).

2.1.4 Discussion

We found that most of the pigs had a significant side bias for manipulating with their snout and curling their tail, indicating lateralization on the individual level. We also found a significant right bias at the population level for the tail curling direction. In contrast, there was no evidence of lateralized foot use in either stepping task since only a minority of the pigs showed significant biases for stepping down or stepping up. Concerning the strength of laterality, we found that pigs were more strongly lateralized for tail curling, followed by manipulation with the snout, for which they were still more strongly lateralized than for the two foot functions.

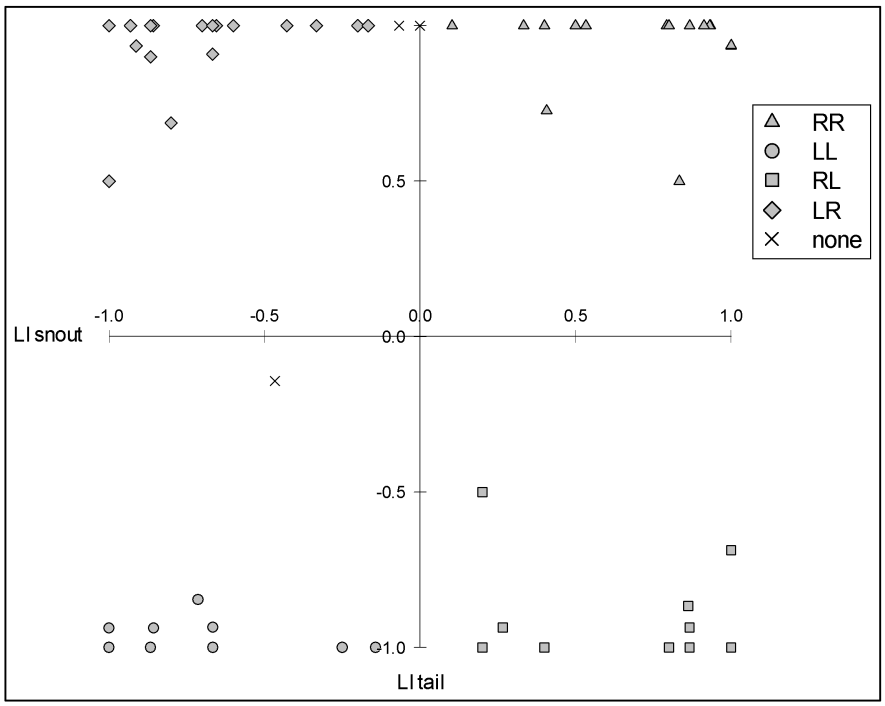

Figure 2.5: Graphical representation of the cluster analysis.

Each individual is positioned on the graph according to its laterality indices (LIs) for snout (x-axis) and tail (y-axis). Positive values reflect a right bias and negative values a left bias. The various filled symbols indicate the different clusters: The first letter indicates the direction (R for right, L for left) of the bias for the snout, the second letter indicates the direction of the bias for the tail. Crosses indicate subjects that were not assigned to any cluster (due to a distance greater than 0.9 from the centre of any cluster).

Lateralization patterns by motor function

Concerning manipulation with the snout, our findings of individual-level lateralization are comparable to findings in other species on motor biases for manipulation, e.g., hand use in primates (Marchant & McGrew, 2013), trunk use in elephants (Martin & Niemitz, 2003) and paw use in other tetrapod species (Bisazza et al., 1998; Ströckens et al., 2013). Mastication has been found to be symmetrical in pigs (Herring, 1976), so it is unlikely that any preferences to eat the food reward on one side of the mouth may have affected the side bias for opening the flap door. Training in other species has been found to modify lateralization patterns, leading to stronger biases (Leliveld et al., 2008) or even shifts in the direction of the biases (Lorincz & Fabre-Thorpe, 1994). Here, we found no trial effect on the lateralized manipulation with the snout, suggesting that the observed lateralized behaviours reflect individual side biases, rather than a learned process during this task. However, though we observed side biases in motor functioning, we cannot exclude the possibility that sensory (olfactory or visual) functions may have affected these side biases. For instance, Hook and Rogers (2008) found no population-level hand preferences in marmosets, but a right eye preference at the group level. These authors suggested that this sensory function interfered with the motor tasks, causing a lack of population-level alignment in hand preferences. In our case, further research is needed on individual nostril and eye prefer-

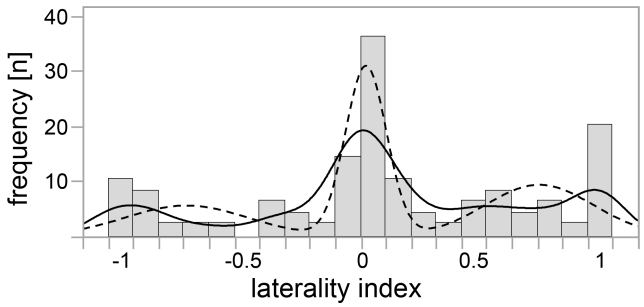

Figure 2.6: Distribution of the individuals according to their combined LI (with an increment of 0.1).

Positive values reflect a right bias and negative values a left bias. The solid line indicates the smooth curve that is plotted in JMP. The dashed line indicates the calculated approximation of a mixture of three normal functions.

ences to determine if sensory processing may have affected the snout biases that we observed.

Concerning the foot, our results are not in line with results in dogs (Tomkins et al., 2010b), where the authors found that a stepping task (consisting of three steps) elicited strong individual preferences and a population bias. Since our stepping task consisted of only one step, this task may not have been challenging enough to elicit foot preferences. Our results are similar to those found in other ungulate species, where no preference in the use of forefeet was found for standing (Austin & Rogers, 2012, 2014) or locomotion (Langbein, 2012; Versace et al., 2007). However, individual foot preferences may still be found for other (more complex) functions since a digging task elicited individual foot preferences in another Artiodactyla species (the reindeer: Espmark & Kinderås, 2002).

Our findings of strong individual biases for tail curling are in line with findings of lateralized tail posture in rats (Rosen et al., 1983) and spider monkeys (Laska & Tutsch, 2000; Stevens et al., 2008). In rats, tail posture was found to be associated with cerebral metabolic asymmetries (Rosen et al., 1984; Ross et al., 1981), meaning tail curling direction may also reflect cerebral asymmetries in pigs. Surprisingly, we found that tail curling is also lateralized at the population level. Lateralized behaviour at the population level is suggested to have evolved as a consequence of an increased need for social coordination (Vallortigara & Rogers, 2005). Indeed, our results are comparable to reports of population-level biases for other motor functions that are used in social interactions, such as communication mechanisms (Meguerditchian et al., 2011; Meguerditchian & Vauclair, 2006; Wallez & Vauclair, 2012). Tail postures are components of the global body posture "which may have a communication value without having necessarily evolved to serve as a signal" (Kiley-Worthington, 1976). Indeed, lateralized tail wagging has been found to reflect a dog's emotional state (Quaranta et al., 2007) as well as affect the emotional state of other dogs (Siniscalchi et al., 2013), suggesting a relevance for intra- and inter-specific interactions (Artelle et al., 2011; Siniscalchi et al., 2013). Additionally, the tail posture of pigs was found to vary according to the emotional context (Reimert et al., 2013), which is the first prerequisite for emotional communication. Because tail curling does not occur in wild boars (Jensen, 2002), it may have emerged in domestic pigs during the domestication process. Similarly, tail up in adult domestic cats has been shown to play a social function that is not found

in adult wild cats (Cafazzo & Natoli, 2009). This behaviour may be partly explained by a need for domestic cats to communicate with humans (Cafazzo & Natoli, 2009). Additionally, domestic pigs show the curled tail more often during interactions with a familiar person (Kleinbeck & McGlone, 1993), suggesting it may have a function in interactions with humans. Based on this, tail posture in pigs may play a role in social interactions, either with conspecifics or with humans; however, this possibility needs to be further investigated. The right population bias could result from a left hemispheric specialization for communication, as is shown in humans (Knecht et al., 2000), and non-human animals (e.g., Meguerditchian & Vauclair, 2006; Siniscalchi et al., 2016). However, this right population bias may also result from a left hemispheric specialization for approach behaviours in rewarding contexts, especially in the context of feeding (e.g., Rogers & Andrew, 2002; Rogers et al., 2013; Siniscalchi et al., 2011). During our tail curling observations, the rewarding context may have consisted of a familiar human entering the home pen with enrichments. Alternatively, the population bias in tail curling may be the result of a morphological directional asymmetry, which is described as an inherited trait where most individuals are asymmetrical in one direction (Palmer, 2004). One example of this is claws of crabs that differ in size (Perez et al., 2015). Future studies on the (muscular) structure of the tail would help increase our understanding of its function and determine if lateralized tail curling is the result of a morphological asymmetry or not. Our work here does not permit us to conclude the exact function of the pig's tail, but the simplicity of measuring its laterality makes this organ very attractive for future laterality research on pigs. This has implications for the common practice of tail docking in pig husbandry to reduce tail biting (Sutherland & Tucker, 2011).

As predicted by the "motor function complexity hypothesis", we found significant differences in the strength of lateralization between the tested motor functions. The fact that we found the weakest biases for the foot use (i.e., stepping up and down) suggests that these motor functions are less complex than the motor functions that involved unpaired organs (snout and tail). As such, our results seem to align with the "organ complexity hypothesis" (Keerthipriya et al., 2015). Surprisingly, tail curling elicited stronger biases than manipulation with the snout, which seems to contradict the "task complexity hypothesis" (Fagot & Vauclair, 1991). However, as discussed above, this finding may be because tail curling behaviour may be a more complex function (with a social-emotional component) than we expected. Alternatively, our results may also support the suggestion of Rogers (2009), which states that the nature of tasks, rather than their complexity, explains the differences found between laterality patterns.

Individual lateralization patterns across motor functions

We found no significant associations between the individual biases for tail curling and for manipulation with the snout. This lack of consistency in direction across both functions may be partially due to the involvement of sensory processing in the snout manipulation function, which we discussed previously. Nevertheless, our results are in line with previous findings in rats (Noonan & Axelrod, 1989) and marmosets (Hook & Rogers, 2008), where no associations between lateralized functions were found. Additionally, Laska (1998) found no associations between the use of tail and hand for grasping in spider monkeys. This led the author to suggest that the lateral biases in hand and tail use are driven by different neural substrates. In addition, sim-

ilar observations have been made in rats (Noonan & Axelrod, 1989) and humans (Bracha et al., 1987; Mohr & Bracha, 2004; Mohr et al., 2003), where the authors suggested that individual left or right hemispheric dominance does not necessarily lead to consistency between every single behavioural asymmetry (Noonan & Axelrod, 1989).

Since laterality is multidimensional, it is suggested that non-human animal studies should take this aspect into account by including several motor functions (Uomini & Hunt, 2016). In this study, we used a cluster analysis to gain more insight into an individual's lateralization pattern across functions. This cluster analysis was based on the individual laterality indices (for the two lateralized functions), which contain more detailed information than the lateralization categories. Therefore, the advantage of the cluster analysis, in contrast to a simple combination of lateralization categories, is that it takes the intra-individual structure for both functions into account (Granero et al., 2016; Tran et al., 2014). The resulting distribution provides a first insight into potentially different brain organizations in domestic pigs with four different laterality types. We found two clusters (RL and LR) where manipulation with the snout and tail curling resulted in different biases. This may indicate that these individuals have no strong tendency to use one hemisphere more than the other. However, since this is a first approximation of an individual's lateralization pattern across functions and is based on only two motor functions, it is also probable that not enough biases are included to identify their individual hemispheric dominance. In contrast, the RR and LL clusters seem to include individuals with a more consistent lateralization pattern across motor functions, suggesting that they are more likely to be right or left hemispheric dominant, respectively. Based on previous reports in humans (Knecht et al., 2000; Pujol et al., 1999) these two groups may also be expected to present a high probability of showing qualitatively different cerebral patterns. Accordingly, these two opposite clusters could also be distinguishable in their personality (Rogers, 2009). In a future publication, we plan to focus on the interactions between motor lateralization patterns and personality indices.

Conclusion

Our study contributes to a better understanding of motor lateralization in pigs in general, and particularly adds an insight into the rarely documented laterality of unpaired organs. We found stronger lateralization patterns for the two unpaired organs compared to the paired organs, supporting the organ complexity hypothesis. Cluster analyses revealed first indications of potentially different brain organizations in pigs, according to their individual lateralization patterns across motor functions. To our knowledge, this study provides the first comprehensive investigation of motor lateralization patterns in the domestic pig. The developed methods provide a good basis to further study laterality in domestic pigs.

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Disclosure statement

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2.2 Second Study: Assessing animal individuality — Links between personality and laterality in pigs

Charlotte Goursot[a], Sandra Düpjan[a], Ellen Kanitz[a], Armin Tuchscherer[b], Birger Puppe[a,c], Lisette M. C. Leliveld[a]*

[a]Institute of Behavioural Physiology, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,
[b]Institute of Genetics and Biometry, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,
[c]Behavioural Sciences, Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany

*Address correspondence to Lisette M. C. Leliveld. E-mail: leliveld@fbn-dummerstorf.de

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Abstract

Animal individuality is challenging to explain because individual differences are regulated by multiple selective forces that lead to unique combinations of characteristics. For instance, the study of personality, a core aspect of individuality, may benefit from integrating other factors underlying individual differences, such as lateralized cerebral processing. Indeed, the approach-withdrawal hypothesis (the left hemisphere controls approach behavior, the right hemisphere controls withdrawal behavior), may account for differences in boldness or exploration between left and right hemispheric dominant individuals. To analyze the relationships between personality and laterality we tested 80 male piglets with established laterality patterns for 2 motor functions (tail curling direction and the side of the snout used for manipulation) and a combined classification integrating both motor functions using cluster analysis. We analyzed basal salivary testosterone and cortisol along with their behavior in standardized tests as pre-established indicators of different personality traits (Boldness, Exploration, Activity, Sociability, and Coping). We found that the direction of the single motor biases showed significant associations with few personality traits. However, the combined laterality classification showed more, and more robust, significant associations with different personality traits compared with the single motor biases. These results supported the approach-withdrawal hypothesis because right-biased pigs were bolder and more explorative in a context of novelty. Additionally, right-biased pigs were more sociable than left-biased pigs. Therefore, the present study indicates that personality is indeed related to lateralized cerebral processing and provides insight into the multifactorial nature of individuality.

Keywords

approach-withdrawal hypothesis; coping; emotion; hemispheric dominance; motor lateralization; temperament

2.2.1 Introduction

Within a population, individuals rarely behave uniformly but rather display complex combinations of different strategies in a variable environment. The maintenance of such variation among phenotypes within a species is hypothesized to be regulated by multiple–sometimes conflicting–selective forces (Sih, 1992). As a consequence, individuals in the same environment can differ in their trade-offs between such selective forces leading to varying combinations of characteristics regulated at different levels (e.g., genetics, physiology, neurobiology, or behavior Sih et al., 2004). For this reason, the basis of individuality is difficult to describe and represents a challenge in various research fields (Pradeu, 2016), for instance animal personality research. Personality is multifactorial and can be defined as a correlated set of individual behavioral and physiological traits that are consistent over time and situations (Réale et al., 2007). Several frameworks have been proposed in an effort to classify them (Dingemanse & Wolf, 2010; Finkemeier et al., 2018; Koolhaas et al., 1999) , such as the five traits model: Boldness (also described as Fearfulness), Exploration, Aggressiveness, Activity, and Sociability (Réale et al., 2007). However, because personality represents only one aspect of individuality, other features underlying individual differences such as physiological (Careau et al., 2008) and neurobiological mechanisms (Freund et al., 2013) should be taken into account (Sih et al., 2015) to better comprehend this phenomenon.

One approach to investigating individual variation in neurobiological mechanisms is the study of individual tendencies to use one hemisphere of the brain more than the other, resulting in individual hemispheric dominance patterns (left or right) that are observable through contralateral individual side preferences in simple motor tasks (Rogers, 2009; see also Rogers & Vallortigara, 2015; Rogers et al., 2013; Vallortigara & Versace, 2017). Indeed, because each hemisphere controls the contralateral side of the body, it is acknowledged that an individual's dominance of one hemisphere results in motor preferences on the contralateral side (Jackson, 2008; Kinsbourne, 1997; Wright & Hardie, 2015). The two hemispheres of the brain specialize in different cognitive processes (referred to as cerebral lateralization), which is believed to enhance individual cerebral efficiency (Ghirlanda & Vallortigara, 2004; Rogers et al., 2004; Vallortigara, 2000, 2006; Vallortigara & Rogers, 2005). For example, the processing of emotions is lateralized with indications that the right hemisphere controls the negative (or withdrawal) emotions and the left hemisphere controls the positive (or approach) emotions (Davidson, 1992b; Quaranta et al., 2007; Siniscalchi et al., 2013; see Leliveld et al., 2013, for a discussion of current hypotheses). Due to these different functions of the two hemispheres, individual tendencies to use one hemisphere more than the other can lead to differences in the response to environmental stimuli (Tops et al., 2017) that are expressed through consistent coping styles or temperaments (Rogers, 2009). As a result, studies on different species have found that right-handed individuals are bolder (Braccini & Caine, 2009; Hopkins & Bennett, 1994), more explorative (Cameron & Rogers,

1999; Gordon & Rogers, 2010) or more sociable (Gordon & Rogers, 2010; Westergaard et al., 2003) than left-handed individuals. Links between the strength of laterality (the degree of dependence on one hemisphere) and personality have also been reported (Found & St. Clair, 2017; Reddon & Hurd, 2009a). Such interactions between laterality and personality could also be exploited in studies on animal welfare (Leliveld et al., 2013; Rogers, 2010). For this reason, an interest in laterality in farm animals is growing (in sheep: Morgante et al., 2007; Morgante et al., 2010; Versace et al., 2007; in cattle: Kappel et al., 2017; Phillips et al., 2015). However, with the exception of domestic fowl, not much is known about laterality in many farm animals.

Like personality, motor lateralization is suggested to be a multifactorial phenomenon expressed through different lateralization patterns within an individual for different motor functions (Forrester, 2017; Healey et al., 1986), which are not necessarily biased in the same direction (Mohr et al., 2003; Noonan & Axelrod, 1989). As a consequence, studies in dogs and chimpanzees found that individual motor lateralization patterns differentially affect personality traits (Barnard et al., 2017; Batt et al., 2009; Hopkins & Bard, 1993), highlighting the importance of a multifactorial approach. Therefore, in our study we aimed to increase our understanding of the complex nature of individuality through an integrative investigation of links between personality and laterality in pigs (*Sus scrofa*).

As a social and generalist species that is one of the most widely distributed mammals in the world (Keiter et al., 2016; Massei & Genov, 2004), the pig represents a suitable model for studying individuality. Because its domestication has been characterized by a long history of unintentional human selection (Marshall et al., 2014) and constant gene flow between European wild boars and Asian domestic pigs (Bosse et al., 2014; Frantz et al., 2015), it remains a species with substantial genetic variability (Amills et al., 2010) and a relatively unchanged behavioral repertoire and cognitive abilities (D'Eath & Turner, 2009; Puppe et al., 2012). Many personality traits have been studied in pigs such as Boldness (Marchant-Forde, 2002; Vetter et al., 2016), Exploration (Brown et al., 2009; van der Kooij et al., 2002), Activity (Krause et al., 2017), Sociability (Forkman et al., 1995) and Coping (Forkman et al., 1995; Hessing et al., 1993). Recently, the first multifactorial classification of the pigs' potential individual hemispheric dominance was made by studying their laterality for two motor 'functions': manipulation with the snout and tail curling, and combining both functions to identify individuals with consistent biases across both motor functions using a cluster analysis (Goursot et al., 2018).

With this previous knowledge on personality and laterality in pigs, we aimed to uncover possible links between these two multifactorial phenomena. To do this, we tested subjects whose individual motor lateralization patterns had been established in Goursot et al. (2018) in a set of personality tests (*Backtest, Human Approach Test, Open Door Test, Open-Field Test, and Novel Object Test*: Forkman et al., 1995; Ruis et al., 2000; van der Kooij et al., 2002). These tests have been shown to meet the requirements for being used as personality tests in that they correlate with each other and are repeatable over time (*Backtest*: Forkman et al., 1995; Zebunke et al., 2017; Zebunke et al., 2015; *Human Approach, Open Door, and Novel Object Tests*: Brown et al., 2009; Ruis et al., 2000; Spoolder et al., 1996; van der Kooij et al., 2002; *Open-Field Test*: Friel et al., 2016). While most parameters measured in these tests can potentially be linked to more than just one personality trait (e.g., latency to contact an unfamiliar object can depend on both Boldness and Exploration), based on the existing body of literature we assigned each parameter to the trait by

which it is influenced most (Table 2.3). For Boldness, we used the latencies to contact a novel human (*Human Approach Test*) or a Novel Object (*Novel Object Test*), or to enter a new environment (*Open Door Test*; Brown et al., 2009; van der Kooij et al., 2002), as well as escape attempts and the proportion of high frequency calls in the *Open-Field Test* (Leliveld et al., 2017; Otten et al., 2007). For Exploration we used exploration of an Open Field (*Open-Field Test*), a Novel Object (*Novel Object Test*) or a novel human (*Human Approach Test*; Brown et al., 2009; van der Kooij et al., 2002). For Activity we used locomotion in the *Open-Field Test* (Zebunke et al., 2017). We also determined the coping style, tested in a *Backtest*, which is not included in the framework of Réale et al. (2007), but is argued to underlie personality in pigs (Finkemeier et al., 2018; Forkman et al., 1995). Additionally, we performed bioacoustic analyses because vocalizations have been found to provide useful insight into pig personality (Friel et al., 2016; Leliveld et al., 2017). The total number of vocalizations in the *Open-Field Test* was used as an indicator of Sociability, because it reflects the motivation to remain close to conspecifics (Forkman et al., 1995; Koolhaas & van Reenen, 2016). Lastly, we determined the testosterone-cortisol ratio from saliva, because the interaction between these hormones has been found to predict any of the following three traits in humans: Boldness, Sociability, or Aggressiveness (Mehta & Prasad, 2015; Terburg et al., 2009). Using this integrative approach, we studied the relationships between individual lateralization patterns and these pre-established personality traits. For this, we compared the left-biased and the right-biased individuals and predicted to find more substantial differences when considering combined motor lateralization patterns than when considering each motor function alone, because animals with consistent biases across motor functions are supposed to have a stronger hemispheric dominance, and therefore are more likely to show more pronounced, consistent individual behavioral patterns. Such patterns could thus be considered indicative of common neurophysiological mechanisms underlying these two aspects of individuality.

2.2.2 Methods

Animals and housing

Details on animals and housing are described in Goursot et al. (2018). In short, the subjects were 80 group-housed pre-pubertal, uncastrated male German Landrace piglets (aged 5–7 weeks during the experimental period) studied in 5 consecutive replicates. Before weaning, the subjects were submitted to 4 *Backtests* to determine their coping style (see description below). Healthy subjects that were classified as having an active (high reactive) or passive (low reactive) coping style—according to the criteria from Zebunke et al. (2015)—were preferentially pre-selected for the study.

The subjects were weaned at 28 days (day 0 in our study) and subsequently housed in a group of 20 pigs (1 group per replicate). From days 4–6 post-weaning, the pigs were habituated to the experimental procedures, particularly to handling and the food reward (chocolate raisins) used in the laterality tests. We selected 16 individuals per replicate based on the following criteria (in order of importance): the absence of illness/injuries, eating a food reward when alone, an active or passive coping style (preferred over an intermediate coping style), relatedness to other subjects (the use of full siblings was avoided where possible), and the absence of extreme nervous-

ness when alone in an unfamiliar environment. Each subject was randomly given an ID-number, which determined the individual tests order throughout the entire experiment. During the laterality tests, the subjects were fed an age-appropriate ration once per day; the rest of the time food was available ad libitum. Water was available ad libitum. The animals had permanent access to a chewing toy, and straw and other rooting materials were provided twice a day for enrichment.

General procedure

The experimental schedule is shown in Figure 2.7. The 4 *Backtests* were performed before weaning, whereas the other 4 personality tests were performed after weaning. On the morning of day 4 post-weaning, the *Human Approach Test* and the *Open Door Test* were performed consecutively in the group. On day 7 post-weaning, the subjects were individually subjected to a combined *Open-Field Test* and *Novel Object Test*. The laterality tests were performed from day 8 to day 21 post-weaning. On days 25–27 post-weaning, saliva was sampled (S1, S2, and S3) for analysis of cortisol and testosterone.

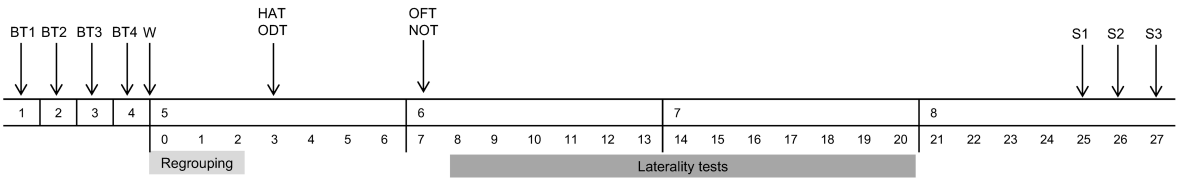

Figure 2.7: Schedule of the general procedure for each replicate.

The numbers in the bottom row indicate the days after weaning (W), whereas the numbers in the top row indicate the weeks of age. BT1-4, *Backtest* 1–4; HAT, *Human Approach Test*; ODT, *Open Door Test*; OFT, *Open-Field Test*; NOT, *Novel Object Test*; and S1-3, saliva samples 1–3.

Laterality tests

Details of the experimental procedures for determining individual motor lateralization patterns are published in Goursot et al. (2018). Briefly, we tested lateralized manipulation with the snout and tail curling direction, and determined laterality for both functions as well as a cluster analysis-based classification of individual lateralization patterns across these 2 motor functions. For manipulation with the snout, the subjects were trained to open a flap door to retrieve a food reward and then forced to use either the left (L) or right (R) side of the snout to open it (details in Goursot et al., 2018). For tail observations, we noted the direction of spontaneous curling of the tail: left curling (L, the tip of the tail is situated to the left of the base), right curling (R, the tip of the tail is situated to the right of the base; details in Goursot et al., 2018). Based on significant individual biases to use one side over the other (tested in a binomial test), individuals were classified as either lateralized (LAT) with a significant bias (L or R) or ambilateral (A, no significant bias) for each motor function. Additionally, for each motor function, a continuous laterality index was calculated as follows:

$$LI = \frac{R-L}{R+L} ,$$

where R is the number of right observations and L is the number of left observations. Individual lateralization patterns across the 2 motor functions (combined laterality classification) were determined with a cluster analysis based on the LI of the 2 functions, identifying those subjects who had a consistent lateralization pattern across functions (e.g., RR: right biased for snout use and tail curling direction) and those who were inconsistent (e.g., RL: right biased for snout use, but left biased in tail curling direction; details in Goursot et al., 2018). In this study, we compared only the subjects with consistent biases for both functions (RR vs. LL, see the section Statistical analyses. As described in Goursot et al. (2018), the majority of the subjects were lateralized for snout use (29 R and 32 L versus 15 A subjects) and tail curling (48 R and 28 L versus 2 A subjects). The cluster analysis revealed 18 RR subjects (right-biased for both functions), 12 LL subjects (left-biased for both functions), and 40 mixed subjects (opposite biases for both functions). The RR subjects and the LL subjects are henceforth referred to as "R-biased pigs" and "L-biased pigs," respectively.

Personality tests

The observed parameters are listed in Table 2.3. Apart from the *Backtest*, all behavioral analyses were made from video recordings using The Observer (The Observer XT 11, Noldus Information Technology bv, The Netherlands), and the data were submitted to an inter-observer reliability test (one of each test was observed by another observer), which resulted in the following kappa indices: 0.89 for the *Open-Field Test*, *Novel Object Test*, and *Human Approach Test*, and 0.99 for the *Open Door Test*. These kappa scores indicate almost perfect agreement between the observations.

Table 2.3: Summary of the parameters measured for each personality trait and by each test: *Human Approach Test* (HAT), *Open Door Test* (ODT), *Open-Field Test* (OFT), *Novel Object Test* (NOT), Saliva Sampling (S), and the *Backtest* (BT).

Trait	Test	Parameter
Boldness	HAT	Latency to approach the novel human (front legs <0.5 m from the novel human) (s)
	ODT	Latency to leave the pen (cross the border with the front legs) (s)
	OFT	Proportion of high frequency calls among all analyzed calls (%)
	OFT	Number of escape attempts (jumping/raising the front legs against the wall) (number/session)
	NOT	Latency to touch the Novel Object (s)
	S	Testosterone/cortisol ratioa (mean of the 3 daily ratios)
Exploration	HAT	Duration in proximity of the novel human (front legs <0.5 m from the novel human) (s)
	OFT	Duration of exploring the Open Field (manipulating the floor or walls with the snout) (s)
	OFT	Frequency of exploring the Open Field (manipulating the floor or walls with the snout) (number/session)
	NOT	Duration of touching the Novel Object with the snout (s)
	NOT	Frequency of touching the Novel Object with the snout (number/session)
Activity	OFT	Duration of locomotion (moving with at least 3 feet) (s)
	OFT	Frequency of locomotion (moving with at least 3 feet) (number/session)
Sociability	OFT	Number of vocalizations (during minutes 3 and 4)
	S	Testosterone/cortisol ratioa (mean of the 3 daily ratios)
Aggressiveness	S	Testosterone/cortisol ratio[a] (mean of the 3 daily ratios)
Coping	BT	Duration of struggling (s)
	BT	Frequency of struggling bouts (number/minute)
	BT	Latency to start struggling (s)

[a] The ratio T/C may be informative on boldness, sociability, or aggressiveness. Please be aware that each parameter can be influenced by several personality traits; we decided, however, to assign it here to the trait with the largest impact.

Backtest

As mentioned previously, we performed 4 *Backtests* at 1-week intervals according to the standardized method of Zebunke et al. (2015). In short, an experimenter put each subject on its back for 1 min and observed its struggling attempts. The mean latency, mean frequency, and mean duration of struggling in the 4 tests were calculated for each individual, because these parameters have been shown to be consistent over time and continuously distributed (Zebunke et al., 2015). The parameters are considered indicators of Coping, whereby a longer duration, higher frequency, and shorter latency indicate a more active coping style.

Human Approach Test and Open Door Test

The *Human Approach Test* and the *Open Door Test* were performed in the home pen on the entire group as described by Leliveld et al. (2017) and were recorded using a video camera centrally positioned above the pen. In short, in the *Human Approach Test*, an unfamiliar person wearing unusual clothing entered the pen, positioned themselves against the wall facing the piglets, and stood still for 5 min. The *Open Door Test* was performed immediately after the *Human Approach Test*; the door of the pen onto the corridor was opened for 5 min, enabling the piglets to leave the pen. For the *Human Approach Test*, we scored the latency and the duration of being in proximity to the human (< 0.5 m). For the *Open Door Test*, we scored the latency to leave the home pen.

Open-Field Test and Novel Object Test

The *Open-Field Test* and the *Novel Object Test* were performed on individual pigs as described in Stracke et al. (2017). In short, these tests occurred in a testing arena (Open Field) located in a sound-attenuated test room. A video camera (connected to a digital video recorder) as well as a microphone (Sennheiser ME64/K6 connected to a Marantz PMD 670 recorder; sampling rate, 44.1 kHz; accuracy, 16 bit; mono) were centrally positioned above the Open Field. Each pig was guided from its home pen into the arena and was left alone. After 5 min, a blue plastic container—the Novel Object—was placed in the center of the Open Field and the animal was observed for another 5 min. The Open Field was cleaned between subjects. For the *Open-Field Test*, we scored the duration and frequency of locomotion and exploration and the frequency of escape attempts. Vocalizations during the *Open-Field Test* were analyzed separately (see below). For the *Novel Object Test*, we scored the latency, frequency, and duration of touching the Novel Object.

Acoustic analyses

Based on an initial count of all vocalizations from the recordings, the third and fourth minutes of the *Open-Field Test* were identified as the periods of maximum vocal response. Each call produced during these 2 min was analyzed in Avisoft-SAS Lab Pro (Version 5.2.05; Avisoft Bioacoustics, Berlin, Germany) using the same methods and settings as described in Leliveld et al. (2016, 2017). We analyzed a total of 13 198 calls. Of these, 1 979 calls had background noise (typically footsteps). Such calls were included in the total number of vocalizations but were excluded from the acoustic analyses, leaving 11 219 calls. Some calls (N = 4,581) were found to consist of a

combination of 2 distinctly different acoustic structures that were easily distinguishable on the oscillogram (mainly grunt-squeals). The different parts of these calls were therefore analyzed separately. The calls were analyzed using the "automatic parameters measurement" option in the spectrogram window (settings: 1,024 FFT length, Hamming window, 50% window overlap, frequency resolution of 43 Hz, temporal resolution of 11.6 ms, and high-pass cut-off frequency at 100 Hz). The following parameters were measured: duration, duration from start to maximum amplitude (% of call duration; DurMax), interval (time from previous call), peak frequency, the minimum and maximum frequency and the resulting bandwidth, 3 quartiles that describe the distribution of energy over the frequency range (Q25, 25%; Q50, 50%; and Q75, 75% of the energy in the frequency range), the number of peaks (above −20 dB, hysteresis: 10 dB), the frequency of the first 2 peaks (F1 and F2), the entropy and the harmonic-to-noise ratio (HNR). The frequency parameters were log-transformed to control for the logarithmic character of animal sound production and sound perception (Cardoso, 2013). Call elements were classified in a cluster analysis using the same procedure as Leliveld et al. (2016, 2017). Parameters that did not correlate strongly with other parameters (Spearman rank correlations, |rs| < 0.9; CORR procedure in SAS (version 9.4; SAS Institute Inc., Cary, NC, USA)) and that followed a multimodal distribution (determined using the KDE procedure) were selected. Accordingly, 8 parameters (duration, DurMax, peak frequency, F1, F2, HNR, maximum frequency, and Q75) were entered into the FASTCLUS procedure of SAS (maxiter = 100, strict = 5). To determine the number of clusters that best represented the data, the Cubic Cluster Criterion (CCC) and the Pseudo F-statistic were examined.

Saliva sampling and analyses

Saliva samples were collected prior to any other intrusion between 08:00 and 08:30 h in the morning on 3 consecutive days by allowing the pigs to chew on synthetic swabs (Salivette® Cortisol, Sarstedt AG & Co., Germany) for 20–30 s. The swabs were placed in Salivette tubes and centrifuged at 2,500 g for 15 min at 4°C. The saliva samples were stored at −20°C until analysis. After thawing, the samples were spun at 2,500 g for 5 min, resulting in a clear supernatant with low viscosity.

The analysis of cortisol concentrations in the saliva was performed in duplicate in 50 µl samples using a commercial Saliva ELISA kit (Demeditec Diagnostics GmbH, Germany) according to the instructions of the manufacturer. The cross-reactivity of the cortisol antiserum has been measured against various compounds and was 63.4% for prednisolone, 10.4% for 11-deoxycortisol, 5.2% for corticosterone, and less than 0.1% for any further competing steroids. The assay was validated for use with porcine saliva. The sensitivity was 0.08 ng/ml, and the intra- and inter-assay coefficients of variation (CV) were 3.4% and 6.6%, respectively.

The saliva testosterone concentration was analyzed in duplicate in 100 µl samples using the Demeditec Saliva ELISA kit (Demeditec Diagnostics GmbH, Germany) according to the manufacturer's guidelines. The cross-reactivities of the antibody to 5α-dihydrotestosterone and androstendione were 23.3% and 1.6%, respectively. The lowest level of testosterone that could be detected by this assay in porcine saliva was 8.9 pg/ml, and the intra- and inter-assay CVs were 5.1% and 12.8%, respectively. After the analysis of cortisol (C) and testosterone (T), a daily T/C

ratio (based on the 3 daily values per parameter) was calculated for each individual. The mean of these daily ratios was then calculated.

Statistical analyses

We used SAS version 9.4 for the statistical analyses. We tested the effect of the direction as well as the effect of strength of laterality on the personality traits. The individual parameters were first analyzed using a 2-way analysis of variance (ANOVA; MIXED procedure) with the individual parameters as dependent variables and the motor bias (L or R for tail, snout, or combined), replicate, and their interaction as fixed factors. Parameters that showed significant interaction effects between replicate and motor bias were considered as not reliable enough for our sample and were therefore excluded from further analyses, as such an interaction can indicate that effects are inconsistent across replicates. For the other parameters, the model was reduced to a 2-way ANOVA (MIXED procedure) with the individual parameters as dependent variables and the motor bias and replicate as fixed factors (without their interaction). Because sample sizes differed among parameters (see the Results section), the power was calculated for a better comparison. For each significant effect, the power (POWER procedure; significance level alpha = 0.05) was calculated based on group means, residual standard deviations, and sample sizes. Significant results with a power above 0.7 (indicating a 70% chance of reproducing the result if the experiment was repeated) were considered to be robust. In order to analyze effects of strength of laterality irrespective of its direction we compared lateralized (LAT) subjects to ambilateral (A) subjects, but we did not perform an ANOVA for tail curling because only 2 individuals were classified as A for this motor function. Because the combined classification was based on 50% of the LI for tail curling, the strength of laterality was also not analyzed for this classification.

2.2.3 Results

Our analyses varied in their sample size for several reasons. As described by Goursot et al. (2018), we had different sample sizes per motor function: 29 R, 32 L, and 15 A subjects for snout use; 48 R, 28 L, and 2 A subjects for tail curling; and 18 RR and 12 LL subjects for the combined classification. In the analysis of the T/C ratio, we included only individuals with all 3 daily T/C ratios available (N = 59). The sample size was also reduced for the *Human Approach Test* (N = 67) and the *Open Door Test* (N = 77) due to difficulties in identifying some individuals during the video analysis, although all the animals approached the human or left the pen. The following results revealed significant interactions of replicate and laterality: the mean frequency and the mean latency of struggling during the *Backtest* for tail bias (frequency: $F_{4,66}$ = 3.77, P = 0.008; latency: $F_{4,66}$ = 4.68, P = 0.002, N = 76) and for the combined laterality classification (frequency: $F_{3,21}$ = 3.30, P = 0.040; latency: $F_{3,21}$=4.64, P = 0.012, N = 30); the T/C ratio ($F_{2,51}$ = 4.16, P = 0.021, N = 59); and the number of vocalizations ($F_{2,68}$ = 3.17, P = 0.048, N = 76) for the strength of snout laterality. These parameters were not taken into account in subsequent analyses with the respective laterality pattern. We will present only significant F-test results; a complete list of statistical results can be found in the Supplementary Material.

Call clusters

Based on the cluster analysis, we found that a 2-cluster option resulted in the highest CCC and Pseudo F-statistic values ($PseudoF$ = 5,798.9, CCC = 382,880). Based on the differences in the frequency values, these 2 clusters were renamed as high frequency calls (mean peak frequency [Hz]: 1,333.26 ± 1,964.83, N = 5 530) and low frequency calls (mean peak frequency [Hz]: 171.71 ± 106.10, N = 5 590). Ninety-nine calls could not be assigned to either of these clusters. Typical calls for each cluster are shown in Figure 2.8.

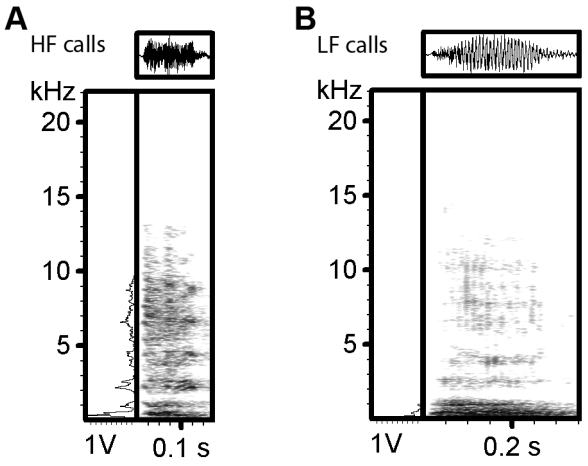

Figure 2.8: Oscillograms (above), power spectra (left), and spectrograms (right) of typical calls (i.e., close to the cluster center) resulting from a cluster analysis ($PseudoF$ = 5,798.9, CCC =382,880, N = 11 219) for the high frequency (HF) cluster (N = 5 530) (**A**) and the low frequency (LF) cluster (N = 5 590) (**B**).

Effect of single motor biases on personality parameters

Concerning the direction of tail laterality (Figure 2.9), the R-tailed individuals vocalized more ($F_{1,70}$ = 4.19, P = 0.044, N = 76, power < 0.7) and produced a higher proportion of high frequency calls ($F_{1,70}$ = 6.14, P = 0.016, N = 76, power = 0.719) during the *Open-Field Test* than the L-tailed individuals.

Concerning the direction of snout laterality (Figure 2.10), the R-snouted individuals produced more vocalizations $F_{1,55}$ = 4.42, P = 0.040, N = 61, power < 0.7) during the *Open-Field Test* and explored the Novel Object more often $F_{1,55}$ = 5.75, P = 0.020, N = 61, power < 0.7) during the *Novel Object Test* than the L-snouted individuals. Concerning the strength of snout laterality (Figure 2.11), the A individuals produced a higher proportion of high frequency calls $F_{1,70}$ = 6.79, P = 0.011, N = 76, power = 0.828) and explored the Open Field longer $F_{1,70}$ = 5.42, P = 0.023, N = 76, power = 0.738) than the LAT individuals in the *Open-Field Test*.

Effect of the combined laterality classification on personality parameters

Concerning the direction of combined laterality (Figure 2.12), the R-biased individuals vocalized more $F_{1,24}$ = 7.14, P = 0.013, N = 30, power = 0.780) during the *Open-Field Test*, and they had

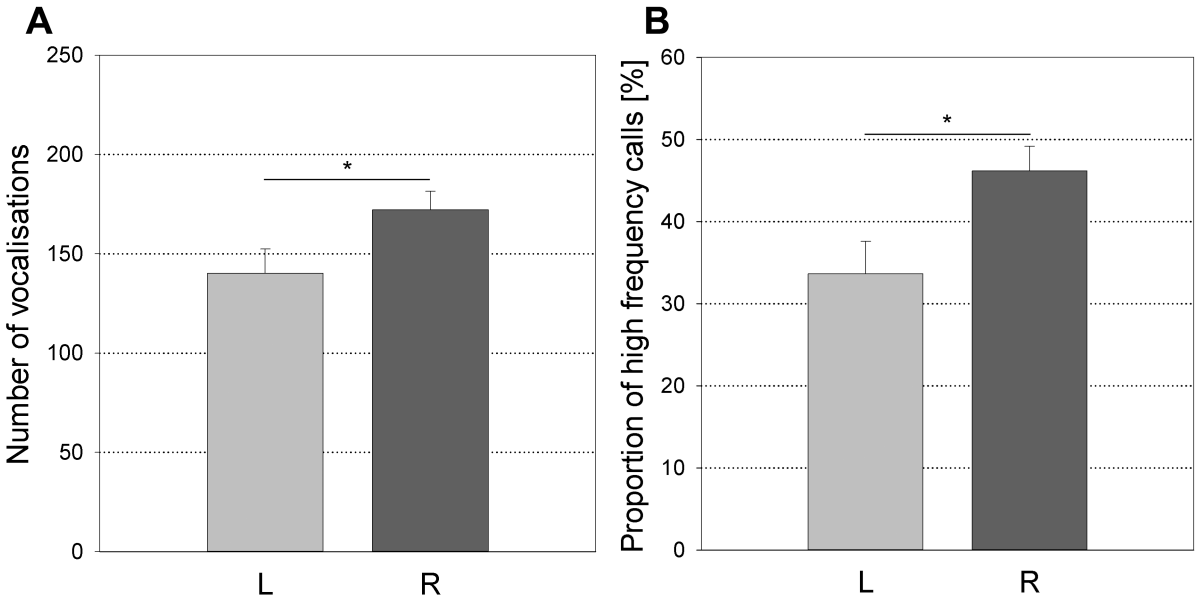

Figure 2.9: Differences for (**A**) the number of vocalizations in the *Open-Field Test* ($F_{1,70}$ = 4.19, P = 0.044, N = 76) and (**B**) the proportion of high frequency calls produced in the *Open-Field Test* ($F_{1,70}$=6.14, P = 0.016, N = 76) between left- (L) and right-tailed (R) individuals (least square means and standard errors). *P < 0.05.

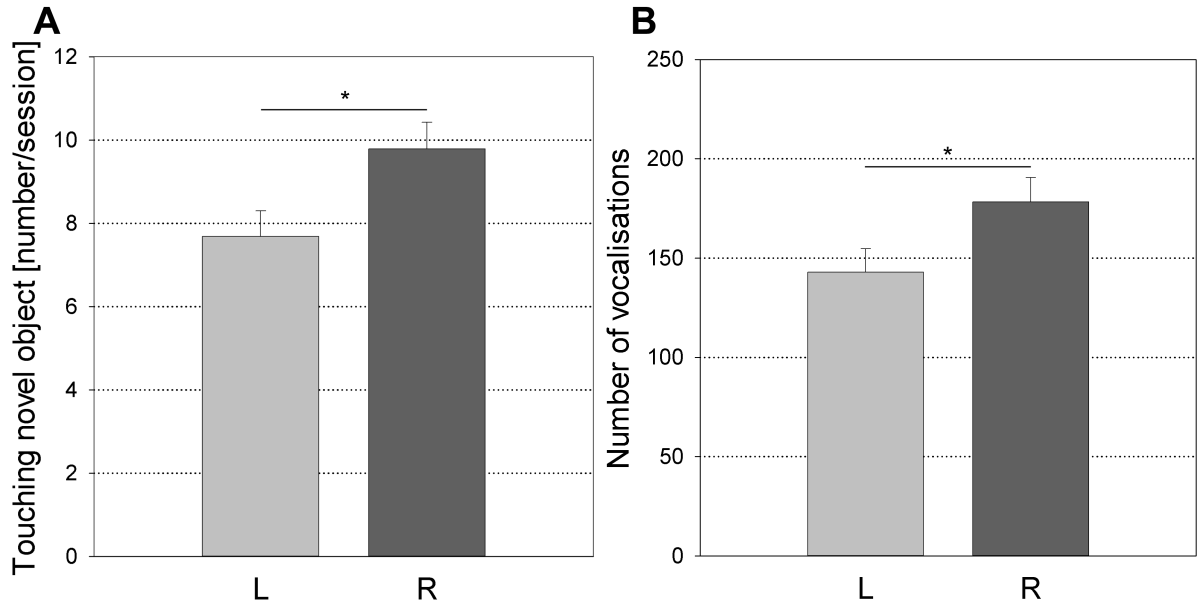

Figure 2.10: Differences for (**A**) the frequency of touching the Novel Object in the *Novel Object Test* ($F_{1,55}$ = 5.75, P = 0.020, N = 61) and (**B**) the number of vocalizations in the *Open-Field Test* ($F_{1,55}$ = 4.42, P = 0.040, N = 61) between the left- (L) and right-snouted (R) individuals (least square means and standard errors). *P < 0.05.

a shorter latency $F_{1,24}$ = 6.38, P = 0.019, N = 30, power = 0.733) and a higher frequency for touching the Novel Object $F_{1,24}$ = 14.92, P = 0.001, N = 30, power = 0.977) during the *Novel Object Test* than the L-biased individuals. In addition, the R-biased individuals struggled longer during the *Backtest* $F_{1,24}$ = 4.90, P = 0.037, N = 30, power < 0.7) than the L-biased individuals.

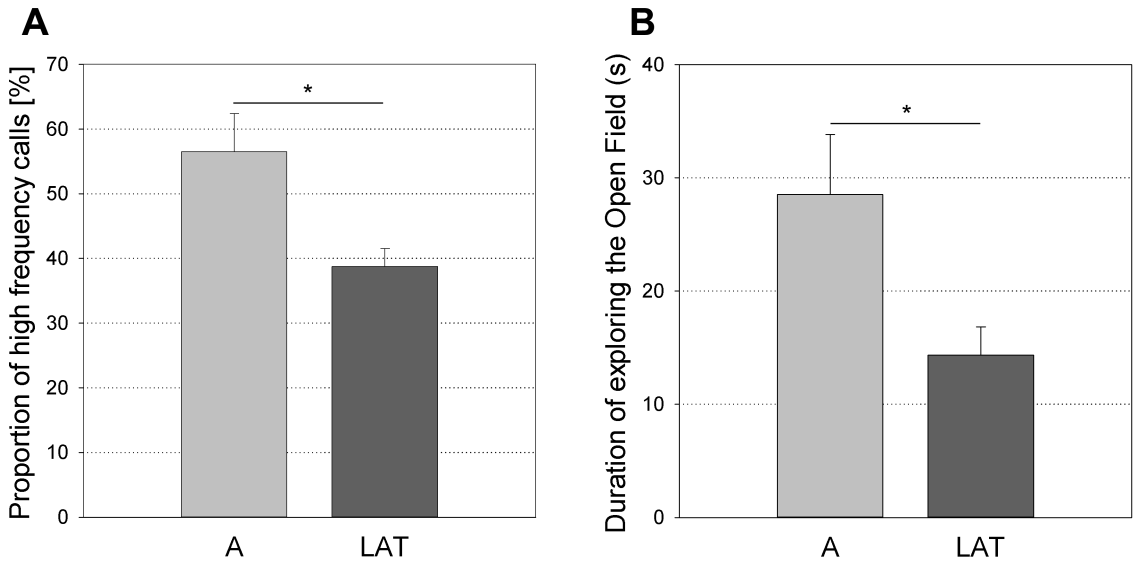

Figure 2.11: Differences for (**A**) the proportion of high frequency calls produced in the *Open-Field Test* ($F_{1,70}$ = 6.79, P = 0.011, N = 76) and (**B**) the duration of exploring the Open Field in the *Open-Field Test* ($F_{1,70}$ = 5.42, P = 0.023, N = 76) between the lateralized (LAT) and ambilateral (A) individuals based on manipulation with the snout (least square means and standard errors). *P < 0.05.

2.2.4 Discussion

Table 2.4: Summary of the significant effects of motor laterality on the different personality traits.

Laterality		Direction		Strength
Personality	Tail	Snout	Combined	Snout
Boldness	**←**		**→**	**↑**
Exploration		→	**→**	**↓**
Activity				
Sociability	→	→	**→**	
Aggressiveness				
Coping			→[a]	

→ individuals with a right bias scored higher on the personality trait, ← individuals with a left bias scored higher on the personality trait, ↑ individuals with a strong bias scored higher on the personality trait, ↓ individual with a weak bias scored higher on the personality trait. Bold arrows indicate results with sufficient power (>0.7).
[a] R biased individuals showed more active coping during the *Backtest*.

We observed different associations between laterality and personality, depending on the per-

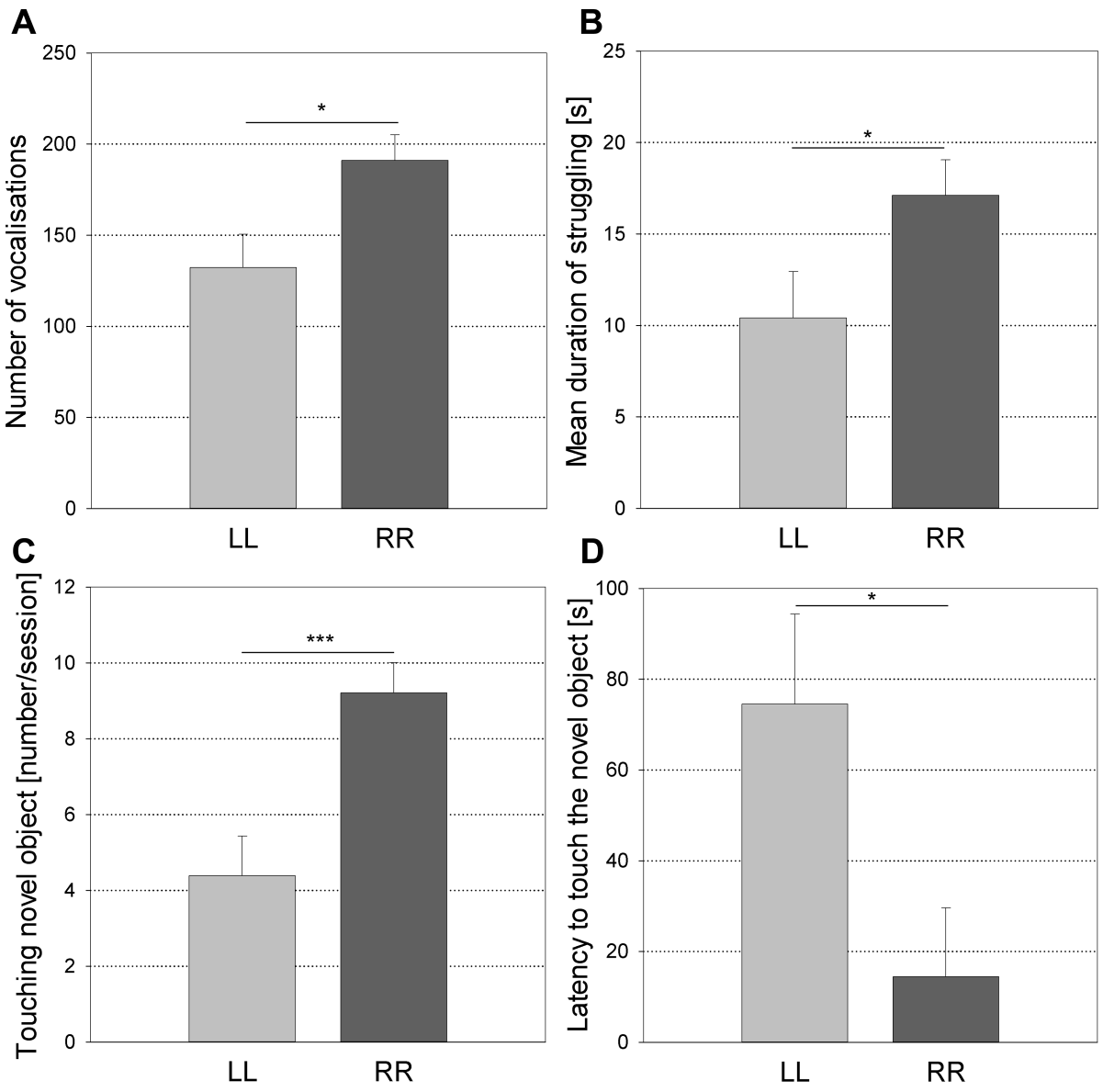

Figure 2.12: Differences for (**A**) the number of vocalizations in the *Open-Field Test* ($F_{1,24}$ = 7.14, P = 0.013, N = 30), (**B**) the duration of struggling during the *Backtest* ($F_{1,24}$ = 4.90, P = 0.037, N = 30), (**C**) the frequency of touching the Novel Object in the *Novel Object Test* ($F_{1,24}$ = 14.92, P < 0.001, N = 30), and (**D**) the latency to touch the Novel Object in the *Novel Object Test* ($F_{1,24}$ = 6.38, P = 0.019, N = 30) between left-biased (LL) and right-biased (RR) pigs (least square means and standard errors). *P < 0.05, ***P < 0.001.

sonality trait and the laterality pattern, as well as the measure of laterality (direction or strength; summarized in Table 2.4). In the following, when discussing each single motor bias, we use the terms of R- or L-snouted or tailed pigs, whereas when describing the combined laterality classification we use the terms R- or L-biased pigs. It appears that the associations depended on the nature of the personality test. Although we found several significant effects of motor laterality on behavior in the *Open-Field Test* and *Novel Object Test*, we did not find any significant effects for the *Human Approach Test* and the *Open Door Test*, which may reflect an effect of group testing (in the *Human Approach Test* and *Open Door Test*) on personality (Koski & Burkart, 2015; Lawrence et

al., 1991). Additionally, we found no significant effects of motor laterality on the T/C ratio. This is not in line with findings of lateralized effects at the cerebral level in humans (Terburg et al., 2009) although there are –to our knowledge– no findings about a link between this ratio and motor laterality. Moreover, it would be beneficial to further investigate this ratio in pig research and test whether, similarly to humans, interactions with status-relevant behaviors can be found (Mehta & Prasad, 2015).

The direction of the single motor bias (snout use and tail curling) showed significant associations with two personality parameters. R-tailed and R-snouted pigs vocalized more in the *Open-Field Test* than L-tailed and L-snouted pigs, which suggests that they were more sociable. R-snouted pigs touched the Novel Object more often in the *Novel Object Test*, suggesting that they were more explorative than L-snouted pigs. However, only one of the significant effects of the direction of the single motor biases on the personality traits reached a sufficient level of power, suggesting that most of these results are not very robust. R-tailed pigs produced a greater proportion of high frequency calls than the L-tailed pigs, indicating that R-tailed pigs were less bold. This seems to contradict findings in other species, where a L bias was associated with increased fearfulness (Braccini & Caine, 2009; Hopkins & Bennett, 1994). However, Gordon and Rogers (2010) found that R handed marmosets also produced more mobbing or alarm calls in a threatening context. The authors discussed that mobbing calls may not only express fear, but are also used to recruit conspecifics (Clara et al., 2008) and therefore interpreted them as an indicator of proactive behavior. Similarly, although in young pigs the high frequency call proportion has been found to reflect fear during isolation (Leliveld et al., 2016) they may also function to recruit adult sows (Weary & Fraser, 1995; Weary et al., 1996). The strength of laterality could only be analyzed for snout use, where it showed two significant associations with Boldness and Exploration. Ambilateral pigs produced a higher proportion of high frequency calls in the *Open-Field Test* than lateralized pigs, suggesting they were less bold (but see discussion above). This is consistent with the findings of reduced Boldness in ambilateral cats and dogs (Branson & Rogers, 2006; McDowell et al., 2016) but in contradiction with the findings of increased boldness in ambilateral elks (Found & St. Clair, 2017). Ambilateral pigs also explored the Open Field longer during the *Open-Field Test*. To our knowledge, this is a first report of a link between exploration and strength of laterality. Both these results had sufficient power and support the idea that strength of laterality can show different associations with different personality traits, like it has been shown for Playfulness, Aggressiveness, and Sociability in dogs (Barnard et al., 2017).

In contrast to the associations with single motor biases, three of the significant associations with the combined laterality classification had sufficient power. R-biased individuals touched the Novel Object more often in the *Novel Object Test*, suggesting they were more explorative, which is consistent with previous studies; R-handed primates explore novel items more than L-handed primates (Braccini & Caine, 2009; Cameron & Rogers, 1999). In addition, R-biased pigs had a shorter latency to touch the Novel Object, suggesting that they were bolder, which is also consistent with previous studies (Braccini & Caine, 2009; Cameron & Rogers, 1999; Gordon & Rogers, 2010; Hopkins & Bennett, 1994; Wright et al., 2004). Our results on Boldness and Exploration are consistent with the approach-withdrawal hypothesis formulated by Davidson (1992b), which also appears to be supported by findings in other non-human species (reviewed in Rogers, 2010): individuals with a supposed left hemispheric dominance – R-biased individuals – approached

more quickly and explored more actively in the context of novelty than individuals with a supposed right hemispheric dominance – L-biased individuals. Additionally, R-biased pigs also vocalized more in the *Open-Field Test*, which may indicate a stronger motivation to regain contact with group members (Koolhaas & van Reenen, 2016; Murphy et al., 2014) and therefore indicate greater Sociability. Alternatively, other authors have suggested (Manteuffel et al., 2004) that the call rate (number of vocalizations) of pigs during the *Open-Field Test*, a context of social isolation, can also be used as an indicator of Fearfulness–that is, lower Boldness according to the framework of Réale et al. (2007). However, the classification into call types may provide more insight into pig personality or emotionality than the call rate only (Friel et al., 2016; Leliveld et al., 2016, 2017). Because no associations were found with the proportion of high frequency calls, it seems more likely that the R-biased subjects were not more fearful but more sociable than the L-biased subjects. Therefore, this result appears to be consistent with previous findings of greater Sociability in R-handed primates (Gordon & Rogers, 2010; Westergaard et al., 2003). We found that R-biased pigs struggled longer than L-biased pigs, which suggests a more active coping style (Zebunke et al., 2017; Zebunke et al., 2015). This would be consistent with the hypothesis that the left hemisphere controls proactive behavior, whereas the right hemisphere controls reactive behavior (Rogers, 2009, 2010). However, we remain cautious in the interpretation of this result because its power was not high and no effects on the other *Backtest* parameters (latency and frequency) could be tested because of significant interactions between the replicate and the combined laterality classification. Taken together, our results support the approach-withdrawal hypothesis: R-biased pigs approached the Novel Object more quickly and more often than L-biased pigs. They also support previous findings in marmosets that suggest that R-handed individuals are more sociable: R-biased pigs were more vocally active than L-biased pigs. This first evidence of complex links between personality and laterality in pigs indicates that the neurophysiological processes underlying individuality (Freund et al., 2013) are shared between the two.

Comparing the single motor biases (tail, snout) and the combined laterality classification, we found that the single motor biases showed weak and often varying associations with the personality traits, while the combined laterality classification showed more robust associations. This is in line with previous findings in dogs and chimpanzees that showed different links with personality depending on the motor function (Barnard et al., 2017; Batt et al., 2009; Hopkins & Bard, 1993), as well as studies in different species that showed that individual hemispheric dominance does not automatically lead to a consistent direction for each individual motor function (Laska, 1998; Mohr et al., 2003; Noonan & Axelrod, 1989). By combining the two motor biases, we expected to provide insight into individual hemispheric dominance, which is suggested to result in individual behavioral patterns (Goursot et al., 2018; Rogers, 2009; Wright & Hardie, 2015). Indeed, the combined laterality classification showed robust associations with 3 personality traits, suggesting that this may be a good approach to the multifactorial nature of laterality and a good alternative to other more demanding approaches (e.g., fMRI) that could be otherwise used to determine the cerebral processing that may underlie differences in hemispheric dominance (Mazoyer et al., 2014) and personality.

To summarize, our study suggests that taking the multifactorial nature of laterality and personality into account will contribute to a better understanding of individuality. Both of these aspects of individuality have implications for the welfare of animals under human care, as they

may influence how an animal perceives and evaluates its environment.

Ethical Statement

The experimental procedure was approved by the ethics committee of the federal state of Mecklenburg-Western Pomerania, Germany (LALLF M-V/TSD/77221.3-2-040/14-1) and adhered to the legal requirements of European Union (directive 2010/63/EU).

Author Contributions

All authors contributed to the planning of the experiments, the data evaluation, and interpretation as well as the preparation of the manuscript. C.G. and L.M.C.L. performed the experiments.

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Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest Statement

The authors declare no conflicts of interest.

2.3 Third Study: Visual laterality in pigs

— Monocular viewing influences emotional reactions in pigs

Charlotte Goursot[a], Sandra Düpjan[a], Armin Tuchscherer[b], Birger Puppe[a,c], Lisette M. C. Leliveld[a]*

[a]Institute of Behavioural Physiology, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,
[b]Institute of Genetics and Biometry, Leibniz Institute for Farm Animal Biology (FBN), Dummerstorf, Germany,
[c]Behavioural Sciences, Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany

*Correspondence: Lisette M. C. Leliveld, Institute of Behavioural Physiology, Leibniz Institute for Farm Animal Biology (FBN), Wilhelm-Stahl-Allee 2, D-18196, Dummerstorf, Germany; E-mail address:leliveld@fbn-dummerstorf.de (L.M.C. Leliveld).

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Highlights

- Monocular viewing tests partially support the emotional valence hypothesis in pigs.
- Monocular viewing had no clear effects on the response to a negative stimulus.
- Covering the right eye attenuated the positive appraisal of a positive stimulus.
- The left hemisphere is important for the quick recognition of a positive stimulus.

Abstract

Understanding animal emotions is an important scientific and ethical question but assessing emotional valence is still considered challenging. As the observation of lateralization (hemispheric asymmetries in structure and/or function) can provide insight into the underlying processes of the cognitive, physiological and behavioural components of emotions, it is a promising approach for studying them. The emotional valence hypothesis states that positive emotions are mostly processed by the left hemisphere, while negative emotions are mostly processed by the right hemisphere. Support for this hypothesis is still not conclusive; therefore, our study tested it in the context of visual laterality for viewing positive or negative emotionally conditioned stimuli. Ninety male piglets were either positively (food-reward) or negatively (mild punishment) conditioned to an object. Afterwards, the object was presented without the reinforcer under three different treatments: patch on the left or right eye (reducing input to the contralateral

hemisphere) or patch between the eyes (the control). Monocular viewing had no clear effects on the negatively conditioned subjects. In contrast, in the positively conditioned group, covering the right eye caused a longer interruption of vocalization, a longer latency to touch the object, a shorter duration of exploring the arena and an increased vagal activity compared to the control. This suggests that reduced processing in the left hemisphere leads to heightened attention that is accompanied by a general orienting response, possibly resulting from a reduced positive appraisal. These findings therefore partially support the emotional valence hypothesis and suggest an important role of the left hemisphere in the quick recognition of a positive stimulus. This study demonstrated that investigating the lateralized processing of emotions can provide insight into the mechanisms of positive appraisal in animals.

Keywords

animal welfare; emotional conditioning; emotional valence hypothesis; heart rate variability

2.3.1 Introduction

Assessing emotions addresses important scientific and ethical issues that could permit a better understanding of (proximate) behavioural control of animals (Gygax, 2017) and that have implications for animal welfare (Boissy et al., 2007). Emotions can be defined as intense and short-lived affective responses to an event and are mostly accompanied by neurophysiological, behavioural, cognitive and subjective changes (Désiré et al., 2002). To objectively assess animal emotions, a two-dimensional framework with arousal and valence as axes has been introduced (Mendl et al., 2010). While arousal can be assessed from physiological reactions (e.g. heart rate increases), it remains difficult to measure and distinguish emotional reactions along the valence axis (Paul et al., 2005). To address this issue, cognitive approaches have been established (e.g. cognitive bias: Harding et al., 2004) and physiological measurements of heart rate and blood pressure variability have been proposed (Krause et al., 2017; von Borell et al., 2007). Lastly, in particular contexts the least arduous way to assess emotional valence remains the use of the behavioural indicators of approach and avoidance (Cabanac, 1992; Dawkins, 1990). Ideally, combining multiple (cognitive, physiological and behavioural) indicators into a componential view would help to increase comprehension of animal emotions (Paul et al., 2005).

The study of lateralization can, arguably, utilize this componential approach to the study of emotions because it has been shown that the cognitive, physiological and behavioural components of emotions are underlain by lateralized cerebral processes in many vertebrate taxa (Leliveld et al., 2013; Rogers, 2010; Rogers et al., 2013). Lateralization refers to the fact that the brain hemispheres can play different roles in many cerebral processes (MacNeilage et al., 2009; Rogers & Vallortigara, 2015; Vallortigara & Versace, 2017), such as in emotional processing. The emotional valence hypothesis states that positive emotions are processed predominantly by the left (L) hemisphere while negative emotions are processed predominantly by the right (R) hemisphere (Demaree et al., 2005; Quaranta et al., 2007; Siniscalchi et al., 2013) and seems to prevail over alternative hypotheses, for example the approach/withdrawal hypothesis (Leliveld et al., 2013). Indeed, many animal taxa show opposite hemispheric dominances for perceiving

food or a predator. However, this may not be explained only by differences in emotional valence since such naturally emotionally charged stimuli often trigger highly aroused states and involve other cognitive functions. Emotional conditioning standardizes the emotional contexts because it permits the use of the same stimulus (for instance an artificial object, unlikely to elicit species-specific behavioural responses) for testing negative and positive emotional processing (Bisazza et al., 2000). Therefore, this approach allows a primary focus on emotional valence (Mendl et al., 2009) without interference from arousal or from other lateralized cerebral processes (e.g. processes involved in flight and feeding; Gupta et al., 2019; Rogers et al., 2013). However, few studies on emotional lateralization have used emotionally conditioned stimuli (e.g. Bisazza et al., 2000; Reddon & Hurd, 2009b). Also, most previous studies have analysed side preferences, while manipulation of lateralized processing by reducing sensory input to one hemisphere (e.g. by covering one eye to induce monocular viewing) allows researchers to investigate the role of each hemisphere in a cerebral process (Vallortigara, 2000). Therefore, our aim was to test the emotional valence hypothesis using emotional conditioning and manipulated monocular viewing.

As pigs, *Sus scrofa*, are acknowledged to be a suitable animal model in physiology and neuroscience (Lind et al., 2007; Swindle & Smith, 2008), they may offer new insights into common patterns of emotional lateralization in vertebrates. The established methods for assessing pigs' emotions often combine behavioural indicators with physiological parameters such as heart rate variability measurements (Düpjan et al., 2011; Krause et al., 2017). In cognitive approaches where pigs were conditioned to stimuli, this combination of indicators was also used to study emotional valence (Stracke et al., 2017; Zebunke et al., 2011). Moreover, in pigs lateralization has been recently found in motor functions and during aggressive encounters (Camerlink et al., 2018a; Goursot et al., 2019; Goursot et al., 2018), making them a good candidate species to test the emotional valence hypothesis.

In this study, we decided to focus on vision as one of the most investigated lateralized modalities (Andrew et al., 1982; Vallortigara, 2000). Pigs have a good visual system (Broom et al., 2009; McLeman et al., 2005) and a high degree of decussation in their optical fibres (87.8%; Herron et al., 1978). This means that visual stimuli are predominantly processed in the contralateral hemisphere (Jones, 1989). Therefore, monocular presentation (which can be achieved by covering the other eye) in this species would guarantee a reduced input to the ipsilateral hemisphere and permit insight into the role of each hemisphere. To test the emotional valence hypothesis in the context of visual laterality in pigs, we studied their behavioural and physiological responses during monocular, compared to binocular, presentation of an emotional conditioned stimulus. We expected that seeing a positive conditioned object with the R eye covered (reduced input to the L hemisphere) would lead to a less positive appraisal than seeing it either with both eyes or with the L eye covered. In addition, we expected that seeing a negative conditioned object with the L eye covered (reduced input to the R hemisphere) would lead to a less negative appraisal than seeing it with both eyes or with the R eye covered.

2.3.2 Methods

Ethical Note

The experimental procedure was approved by the ethics committee of the federal state of Mecklenburg-Western Pomerania, Germany (LALLF M-V/TSD/7221.3-2-046/14) and adhered to the legal requirements of the European Union (directive 2010/63/EU) and also the ASAB/ABS guidelines for the use of animals in research. Reduction of animals used was guaranteed by performing a sample size determination using the SAS Power and Sample Size application, a desktop application that provides power and sample size computations for a variety of statistical analyses (e.g. analyses of variance and linear models). Refinement was achieved by providing environmental enrichment exceeding the usual chewing toys (see section Subjects, housing and husbandry), and by reducing social isolation to a minimum (allowing acoustic contact where possible).

Subjects, Housing and Husbandry

The study was conducted at the Experimental Facility for Pigs (EAS) of the Leibniz Institute for Farm Animal Biology (FBN) in Dummerstorf, Germany. The subjects were 90 prepubertal, uncastrated male German Landrace piglets 5-6 weeks old. Experiments were performed with five consecutive replicates between August and November 2015. At 4 weeks of age, 20 piglets per replicate were preselected from a greater pool based on their health status, absence of injuries and weight (>5 kg). When possible, the number of full siblings was set at two per sow or (if not enough sows were available) at four per sow (always even numbers for a pairwise design). The preselected piglets were weaned and grouped in a pen (2.50 x 3.95 m) with fully slatted plastic floors and two solid concrete sections. They had access to food and water ad libitum. Straw and some other physical enrichment (buckets, rags, etc.) were provided twice a day during the entire experimental period, except on days 5 and 6, when no experiments took place. For the experiment, 18 subjects consisting of nine pairs of full siblings per replicate (90 subjects in 45 pairs in total) were randomly selected among the preselected group and divided into two groups: the positive and the negative conditioning group (nine subjects per replicate, 45 subjects in total per conditioning group, balanced for kinship). Each subject was randomly given an ID number, which determined the individual test order throughout the experiment. The experimental procedure is summarized in Figure 2.13. Three days after weaning (day 1), the experiment began and lasted for 12 days. The pigs were habituated to being handled by the experimenters (two sessions of 1 h per day on days 1-3), to the food reward and to the experimental set-up (see section Habituation below).

Experimental Set-up

The conditioning took place in a conditioning arena (1.50 x 1.50 m) that was connected to the home pen through a corridor (0.51 x 1.85 m). A sliding guillotine door (0.39 x 0.45 m) that could be operated from the corridor was used to provide access to the arena. The tests took place in a test arena (3 x 3 m) located in a sound-attenuated room, with a microphone (Sennheiser

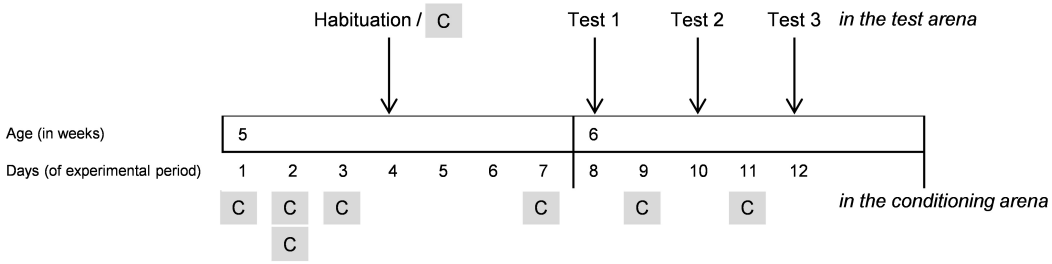

Figure 2.13: Schedule of the general procedure for each replicate.

The numbers in the bottom row indicate the days of the experimental period; the numbers in the top row indicate age (weeks). The letter C indicates when a conditioning session took place. The position of the text indicates where the different tests and conditioning sessions took place: test arena (in the top of the schedule) or conditioning arena (in the bottom of the schedule).

ME64/K6) placed centrally above and connected to a digital audio recorder (Marantz PMD 670; sampling rate: 44.1 kHz; accuracy: 16 bit; mono). Two cameras, connected to a digital video recorder, were positioned centrally above both arenas. The object was an orange ball hanging from a metal cord that was lowered into the arena from outside. A preparation box (94.5 x 40 cm and 73 cm high) was used for fixing the heart rate measurement belt.

Conditioning

Conditioning started on day 1 (one session on days 1 and 3, two sessions on day 2) in the conditioning arena. To optimize learning, the conditioning occurred in groups of three subjects that were randomly chosen for each session. During the first and fourth conditioning sessions (days 1 and 3), a heart rate measurement belt connected to a heart rate monitor via Bluetooth (Polar system; measurement belt: WearLink + H3 sensor; monitor: RS800CX; Polar Electro Oy, Kempele, Finland) was fitted on the pigs in the preparation box so that they became accustomed to the procedure. The measurement belt was fixed directly behind the front legs with the transmitter positioned in the left 'armpit' as described in Düpjan et al. (2011). Ultrasound transmission gel (Henry Schein, Melville, NY, U.S.A.) was used to improve contact with the skin. A conditioning session consisted of four trials (except on day 4 in the test arena, only two trials) of 1 min each and with a break of 1 min between trials: in total, a session lasted 8 min (4 min on day 4). During a trial, the object (an orange ball, Zeus Bomber dog toy, 18 cm diameter) was lowered into the middle of the conditioning (or test) arena by the experimenter. For positive conditioning, 2 tablespoons of food reward were spread on the object (positive reinforcer: a viscous mixture of dry food (Porcistart, Trede und von Pein, Itzehoe, Germany) with apple juice), from which the pigs could eat directly. For the negative conditioning, we used the same methods validated in Düpjan et al. (2017): a plastic bag was waved by the experimenter above or in front of the subjects until they showed a clear avoidance response. This negative reinforcer was given as soon as one pig touched the object, except during the last trial of the first conditioning session, the first trial of the conditioning session on day 4 and one pseudorandomly chosen trial during all other conditioning sessions (with the same trial for a maximum of two sessions) in which it was given at a randomized time point. This procedure allowed us to give the reinforcer at least once

per session. Before and after each session, the subjects received a small portion of food reward in the corridor to maintain their motivation to participate in the conditioning sessions. To prevent extinction of the emotional response during the tests, the pigs received further conditioning systematically 1 day before each test (days 7, 9 and 11; one session per day).

Habituation

On day 4, the pigs were habituated to the test procedure in the test arena and underwent one conditioning session there. Each pig was guided from its home pen into the sound-attenuated room. In the entrance area, in the preparation box, a heart rate measurement belt was fitted on the subject, using the same procedure as during the conditioning sessions, and an eye patch (6.5 x 4.5 cm cotton textile fixed with adhesive tape (Fixomull stretch, BSN medical GmbH, Germany)) was fixed on its forehead so that the pigs became accustomed to the test procedure. After this, the pig was guided into the test arena and left alone for 4 min, while the experimenter stayed in the room, outside the test arena, hidden from view.

Tests

On days 8, 10 and 12, the subjects were individually tested with three different treatments (Figure 2.14). Before the test sessions, subjects were fitted with the heart rate measurement belt and, according to the treatment, an eye patch either covering the left eye (left eye covered, LEC), right eye (right eye covered, REC) or on the forehead as a control (binocular viewing, BIN). After this, the pig was guided into the test arena and left alone for 4 min, while the experimenter stayed in the room, outside the test arena, hidden from view (same as in the habituation procedure). The object, without the reinforcer, was lowered in the middle of the test arena after 2 min and removed again after 1 min by the experimenter. The order of the three treatments was pseudorandomly chosen for each individual and was balanced across subjects, as far as possible. In our statistical analyses, we included the minute before ('Pre'), during ('Object') and after ('Post') the presentation of the object. Owing to illness, one subject could not participate during the last test day (Test 3). Additionally, for technical reasons, six entire test sessions and the Post minute from two sessions were excluded from the analyses.

Behavioural Analyses

For behavioural analyses from video, we used The Observer (The Observer XT 12, Noldus Information Technology bv, Wagenigen, The Netherlands). Based on the behavioural observations, the following parameters were analysed: first, parameters concerning behaviours that occurred during the whole test, which were duration of locomotion and of exploration of the arena, as well as number of vocalizations; second, parameters concerning behaviours that exclusively occurred during the object presentation, which were duration, frequency and latency of touching the object and latency to vocalize after the introduction of the object. If a subject did not vocalize or touch the object during its presentation, the latency was set at 60 s. Since each video observation represented one subject during one test, we obtained 269 video observations (see Results)

Treatment / Contralateral input	LEC	REC	BIN
Reduced	RH	LH	none
Unaffected	LH	RH	LH & RH

Figure 2.14: Summary of the treatments with an overview of the visual contralateral input to each hemisphere.

When the left eye was covered with a patch (LEC) the contralateral input to the right hemisphere (RH) was reduced while the input to the left hemisphere (LH) was unaffected. The opposite was true when the right eye was covered (REC). In the control treatment (BIN, binocular viewing) the patch was fixed on the subject's forehead and the input to both hemispheres was unaffected.

which were analysed by two different observers (blind for the conditioning group). Before the beginning of the analyses, an interobserver reliability analysis was performed: three observations were analysed by both observers as well as a third observer and were compared. All combined comparisons (observer 1-observer 2; observer 1-observer 3; observer 2-observer 3) resulted in a kappa of 0.83, which indicates a very good agreement between the three observers.

Heart Rate Measurements

When a measurement was started, the heart rate monitor made a sound. Later, in the analysis, this sound was used to synchronize the heart rate measurements with the video and acoustic recordings. Using the Polar system, we measured the interbeat (R–R) intervals. For the corrections, we used the same methods described in Leliveld et al. (2016). In short, using 1 min intervals, data were corrected for artefacts (Software: Polar Precision Performance SW, version 4.03.040; settings: very low sensitivity, peak detection on, minimal protection zone of 20) or excluded if artefacts comprised more than 10% of the data or gaps of more than 3 s occurred. After corrections, sections with a linear development for five or more consecutive R-R intervals (indicating that a reliable correction was not possible) were excluded as well. Owing to these artefacts in the HR measurements, 3873 (from 6480) 10 s intervals were excluded from the HR analyses. The mean heart rate and heart rate variability parameters were calculated in 10 s intervals. The heart rate variability parameters that were derived in the time domain were the standard deviation of the interbeat intervals (SDNN, which indicates both sympathetic and parasympathetic activity), the root mean square of successive differences between interbeat intervals (RMSSD, which indicates parasympathetic activity) and the ratio of these two (RMSSD:SDNN, which reflects the balance of the autonomic nervous system). Means of the available 10 s values were then calculated for the Pre, Object and Post minutes.

Statistical Analyses

For statistical analyses, we used the SAS System for Windows, version 9.4 (SAS Institute Inc., Cary, NC, U.S.A.). We tested the effects of conditioning (positive or negative), treatment (BIN, LEC or REC) and minute (Pre, Object or Post) and their interactions. The behavioural parameters and heart rate variability parameters were analysed by repeated measurement analyses of variance (ANOVA) with the MIXED procedure of SAS/STAT software using a model with replicate, conditioning, treatment, minute and the interaction of conditioning*treatment*minute as fixed factors. Additionally, the duration of locomotion was included as a covariate for the heart rate parameters. Object-related parameters were analysed for the minute of the object presentation only (PROC MIXED for durations and PROC GLIMMIX for the frequency for touching the object), with replicate, conditioning, treatment and the interaction of conditioning*treatment as fixed factors. Test order and sow (effect of kin) were set as random effects. Repeated measures on the same animal were taken into account by using the REPEATED statement in the MIXED procedure or the RANDOM _residual_ statement of the GLIMMIX procedure. Pairwise comparisons were made with Tukey-Kramer tests (i.e. adjusting P values to correct for multiple testing) and by using the SLICE option for performing a partitioned analysis of the least square means for an interaction that permits the selection of only the relevant comparisons (e.g. within a conditioning group, within the same treatment or within the same minute). Effects and differences were considered significant if P <0.05.

2.3.3 Results

The sample size consisted of 90 animals (N) with varying repeated measurements (Ni) according to the type of parameters (Ni = 3 for object-related parameters - 3 test sessions x 1 minute; Ni = 9 for the other behavioural parameters and for the HR variability parameters - 3 test sessions x 3 minutes). This resulted in different total numbers of observations ($NObs$) according to the type of parameters: $NObs$ = 263 for the object-related parameters, $NObs$ = 787 for the other behavioural parameters and $NObs$ = 372 for the heart rate variability parameters. Comparisons between conditioning groups are presented in the Appendix.

Effect of Eye Covering after Positive Conditioning

Concerning the object-related parameters within the positively conditioned group (Figure 2.15), REC led to a longer latency to touch the object (t_{169} = -2.96, P_{Tukey} = 0.010) and to vocalize after its introduction (t_{118} = -3.24, P_{Tukey} = 0.004) than BIN.

The interactions between minute and treatment within the positively conditioned group for all parameters are shown in Table 2.5. During the Pre minute, all treatments differed significantly from each other in RMSSD, with LEC causing the lowest RMSSD and REC the highest (BIN-REC: t_{182} = -3.02, P_{Tukey} = 0.009; BIN-LEC: t_{85} = 7.82, P_{Tukey} < 0.001; REC-LEC: t_{318} = 10.09, P_{Tukey} < 0.001). During the object presentation, REC led to the highest RMSSD (BIN-REC: t_{47} = -3.14, P_{Tukey} = 0.007; REC-LEC: t_{48} = 3.77, P_{Tukey} < 0.001) and to the least exploration of the arena (BIN-REC: t_{139} = 2.71, P_{Tukey} = 0.020; REC-LEC: t_{136} = -2.66, P_{Tukey} = 0.023) compared to the other treatments. Within BIN, both the RMSSD (t_{49} = -3.23, P_{Tukey} = 0.005) and the time

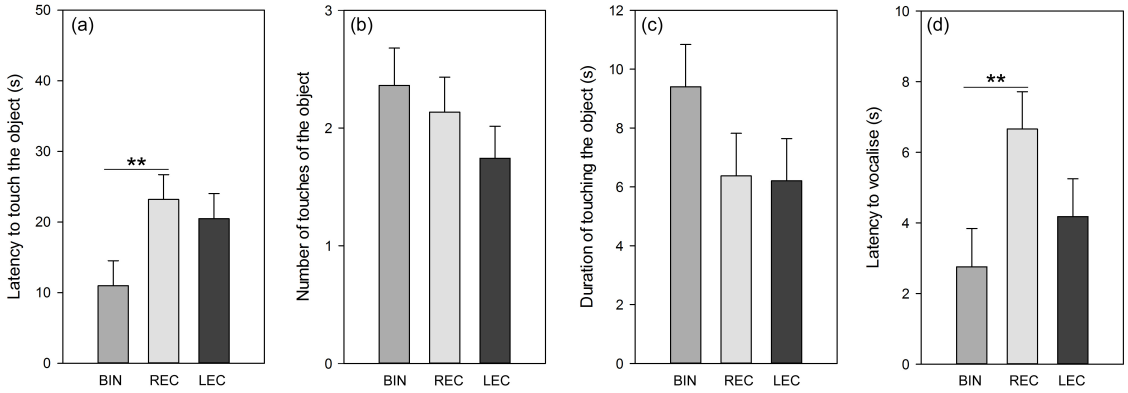

Figure 2.15: Least square means and SEs of (a) the latency to touch, (b) number of touches, (c) duration of touching the object and (d) latency to vocalize after the introduction of the object to the positively conditioned subjects according to the treatment (with either the right (REC) or left (LEC) eye covered or binocular (BIN) viewing). $^{**}P_{Tukey} < 0.01$.

spent exploring the arena (t_{205} = -2.95, P_{Tukey} = 0.010) decreased significantly from the Pre to the Post minute. Within REC, the time spent exploring the arena also decreased significantly (t_{243} = 3.21, P_{Tukey} = 0.004) from the Pre to the Object minute and the RMSSD increased significantly (t_{51} = 3.49, P_{Tukey} = 0.002) from the Pre to the Post minute. Within LEC, the RMSSD (t_{61} = 5.91, $P_{Tukey} < 0.001$) and the duration of locomotion (t_{242} = 2.74, P_{Tukey} = 0.019) also increased significantly from the Pre to the Post minute.

Effect of Eye Covering after Negative Conditioning

Within the negatively conditioned group, we found no significant differences between the treatments among the object-related parameters (Figure 2.16). The interactions between minute and treatment within the negatively conditioned group for all parameters are shown in Table 2.6. During the Pre minute, REC led to the lowest RMSSD compared to the other treatments (BIN-REC: t_{190} = 6.17, $P_{Tukey} < 0.001$; REC-LEC: t_{349} = -3.76, $P_{Tukey} < 0.001$), and LEC led to significantly more vocalizations (t_{205} = -2.94, P_{Tukey} = 0.010) than BIN. The latter effect was also present during the Object (t_{231} = -3.24, P_{Tukey} = 0.004) and Post (t_{297} = -3.04, P_{Tukey} = 0.008) minutes.

Within BIN, the number of vocalizations increased significantly (t_{236} = 2.92, P_{Tukey} = 0.011) from the Pre to the Post minute. Within REC, the number of vocalizations also increased significantly from the Pre to the Post minute (t_{235} = 2.44, P_{Tukey} = 0.041), and the duration spent exploring the arena decreased significantly (t_{243} = 2.74, P_{Tukey} = 0.018) from the Pre to the Object minute. Within LEC, the subjects significantly increased their locomotion (t_{250} = -2.41, P_{Tukey} = 0.045) from the Pre to the Object minute. Additionally, the time spent exploring decreased significantly from the Pre to the Object minute (t_{240} = 2.68, P_{Tukey} = 0.022), as well as from the Pre to the Post minute (t_{198} = -2.68, P_{Tukey} = 0.022).

Table 2.5: Behavioural and physiological responses of the positively conditioned subjects by treatment and minute

Parameter	Minute	BIN	REC	LEC
Number of vocalizations	Pre	41.84 ± 5.40	40.40 ± 5.38	41.49 ± 5.39
	Object	42.61 ± 5.32	41.77 ± 5.29	46.06 ± 5.31
	Post	46.57 ± 5.20	46.88 ± 5.19	47.15 ± 5.19
Duration of exploring the arena (s)	Pre	**6.88 ± 1.32**^{A}	**5.26 ± 1.31**^{A}	5.09 ± 1.33
	Object	**4.89 ± 1.04**$^{a/A,B}$	**1.97 ± 1.03**$^{b/B}$	**4.92 ± 1.04**^{a}
	Post	**3.29 ± 1.07**^{B}	3.14 ± 1.06^{A,B}	4.35 ± 1.06
Duration of locomotion (s)	Pre	31.01 ± 1.87	30.01 ± 1.86	**28.74 ± 1.87**^{A}
	Object	32.48 ± 1.85	31.50 ± 1.84	32.51 ± 1.85^{A,B}
	Post	32.30 ± 1.71	32.20 ± 1.70	**32.87 ± 1.71**^{B}
Heart rate (bpm)	Pre	183.64 ± 6.82	173.47 ± 5.69	182.80 ± 5.87
	Object	182.84 ± 7.45	174.05 ± 5.94	183.56 ± 6.70
	Post	185.81 ± 9.44	181.40 ± 7.60	186.97 ± 10.14
RMSSD (ms)	Pre	**16.98 ± 1.17**$^{b/B}$	**18.99 ± 1.17**$^{c/A}$	**12.28 ± 1.16**$^{a/A}$
	Object	**15.63 ± 1.27**$^{a/A,B}$	**20.43 ± 1.26**$^{b/A,B}$	**14.71 ± 1.27**$^{a/A,B}$
	Post	**14.03 ± 1.05**$^{a/A}$	**22.14 ± 1.02**$^{c/B}$	**17.33 ± 1.02**$^{b/B}$
RMSSD:SDNN	Pre	0.71 ± 0.04	0.64 ± 0.03	0.64 ± 0.04
	Object	0.70 ± 0.03	0.72 ± 0.04	0.70 ± 0.04
	Post	0.63 ± 0.03	0.64 ± 0.03	0.65 ± 0.03

Least square means are shown ± SEs. Minute: before (Pre), during (Object) and after (Post) the object was presented. Treatments: either the right (REC) or left (LEC) eye covered, or binocular (BIN) viewing. RMSSD: root mean square of successive differences between interbeat intervals; SDNN: standard deviation of the interbeat intervals. The lowercase letters indicate differences between the treatments within a minute. The uppercase letters indicate differences between the minutes within a treatment. The significant differences (P_{Tukey}<0.05) are in bold.

2.3.4 Discussion

Our results show that within each conditioning group, the subjects differed in their behavioural and physiological reactions during the tests depending on the monocular treatment, which indicates that monocular viewing influences emotional reactions in pigs: covering the R eye (REC; leading to reduced input to the L hemisphere) influenced the positively conditioned subjects more than the other treatments (seeing with both eyes or with the L eye covered), while covering the L eye (LEC; leading to reduced input to the R hemisphere) influenced the negatively conditioned subjects more than the other treatments (seeing with both eyes or with the R eye covered). Within the binocular (BIN; control) treatment, the positively conditioned subjects showed a shorter latency and longer duration of touching the object and touched the object more frequently than the negatively conditioned subjects (see Appendix, Figure 2.17). This validates our conditioning paradigm as has already been applied in previous studies (Düpjan et al., 2017; Leliveld et al., 2016).

REC influenced the reaction of the **positively conditioned subjects** compared to BIN. Indeed, REC led to a longer latency to touch the object in comparison to BIN which suggests that the object was perceived as less rewarding (De Boyer Des Roches et al., 2008). Additionally, REC led to a longer latency to vocalize compared to BIN. An interruption in vocalizations has been suggested to reflect a heightened state of attention (Düpjan et al., 2011). Taken together, these longer latencies to vocalize and to touch the object more resembled the responses after negative con-

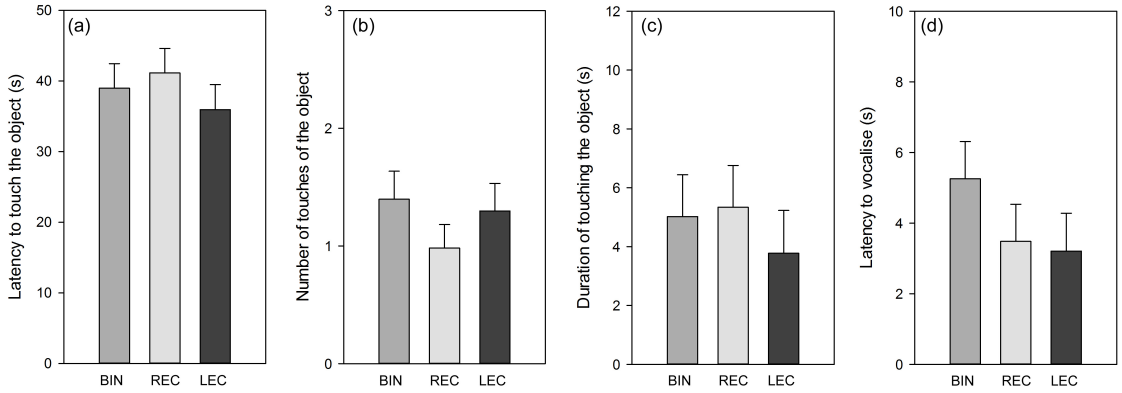

Figure 2.16: Least square means and SEs of (a) the latency to touch, (b) number of touches, (c) duration of touching the object and (d) latency to vocalize after the introduction of the object to the negatively conditioned subjects according to the treatment (with either the right (REC) or left (LEC) eye covered or binocular (BIN) viewing).

Table 2.6: Behavioural and physiological responses of the negatively conditioned subjects by treatment and minute

Parameter	Minute	BIN	REC	LEC
Number of vocalizations	Pre	**31.47 ± 5.37**$^{a/A}$	**36.8 ± 5.37**$^{a,b/A}$	**40.63 ± 5.39**^{b}
	Object	**36.73 ± 5.29**$^{a/A,B}$	41.03 ± 5.28$^{a,b/A,B}$	**45.42 ± 5.31**^{b}
	Post	**39.86 ± 5.17**$^{a/B}$	**43.80 ± 5.17**$^{a,b/B}$	**46.45 ± 5.18**^{b}
Duration of exploring the arena (s)	Pre	4.44 ± 1.31	**6.40 ± 1.31**^{A}	**7.63 ± 1.33**^{A}
	Object	3.54 ± 1.03	**3.62 ± 1.03**^{B}	**4.86 ± 1.04**^{B}
	Post	4.83 ± 1.05	4.31 ± 1.05^{A,B}	**4.40 ± 1.07**^{B}
Duration of locomotion (s)	Pre	30.38 ± 1.85	29.38 ± 1.85	**29.15 ± 1.88**^{A}
	Object	32.96 ± 1.83	31.95 ± 1.83	**33.06 ± 1.85**^{B}
	Post	30.73 ± 1.69	31.07 ± 1.69	31.57 ± 1.70^{A,B}
Heart rate (bpm)	Pre	167.62 ± 6.42	173.74 ± 6.61	174.73 ± 6.02
	Object	168.83 ± 7.04	176.09 ± 7.39	176.00 ± 6.48
	Post	163.61 ± 8.21	173.99 ± 8.94	171.02 ± 8.84
RMSSD (ms)	Pre	**20.12 ± 1.21**^{a}	**16.47 ± 1.20**^{b}	**19.19 ± 1.26**^{a}
	Object	18.66 ± 1.29	16.20 ± 1.27	18.06 ± 1.33
	Post	19.76 ± 1.12	17.97 ± 1.07	18.33 ± 1.05
RMSSD:SDNN	Pre	0.70 ± 0.04	0.63 ± 0.04	0.65 ± 0.04
	Object	0.67 ± 0.03	0.62 ± 0.04	0.66 ± 0.04
	Post	0.64 ± 0.03	0.62 ± 0.03	0.62 ± 0.03

Least square means are shown ± SEs. Minute: before (Pre), during (Object) and after (Post) the object was presented. Treatments: either the right (REC) or left (LEC) eye covered, or binocular (BIN) viewing. RMSSD: root mean square of successive differences between interbeat intervals; SDNN: standard deviation of the interbeat intervals. The lowercase letters indicate differences between the treatments within a minute. The uppercase letters indicate differences between the minutes within a treatment. The significant differences (P_{Tukey}<0.05) are in bold.

ditioning than after positive conditioning in the control treatment (see Appendix, Figure 2.17), which may therefore indicate a less positive reaction. Additionally, REC induced the shortest duration of exploring the arena during object presentation. This was due to a significant decrease in exploration compared to the Pre minute, which was stronger than for BIN. Reduced explo-

ration in pigs may indicate either decreased arousal or increased anxiety (Donald et al., 2011). However, this behavioural response, combined with the increased latencies to touch the object and vocalize, could also reflect an increased attention directed to the object. Concerning heart rate variability, REC systematically led to the highest values in RMSSD compared to the other treatments, reflecting a higher vagal activity of the autonomic nervous system (von Borell et al., 2007). This effect, in the absence of changes in heart rate, can be assumed to be accompanied by a mild sympathetic activation and has been interpreted as a general orienting response (Désiré et al., 2004). Interestingly, REC led to an increase in RMSSD over time, from the Pre minute to the Post minute, without any changes in the heart rate, while the opposite trend occurred for BIN. However, since the same was found for LEC this indicates an effect of monocular testing. It may reflect a general orienting response (Désiré et al., 2004) caused by disorientation in the arena resulting from impaired depth perception (Hughes, 1977).

REC showed fewer effects on the **negatively conditioned subjects**. It led to a significant decrease in exploration during the object presentation. Since LEC had the same effect this might reflect an increased anxiety (Donald et al., 2011) due to impaired depth perception. Apart from that, we only found that in the Pre minute, the RMSSD was lower for REC compared to BIN. This may indicate that REC influenced the reaction to the general situation of social isolation or to the anticipation of the stimulus. However, this result is difficult to interpret because it was not accompanied by any significant effects on the behaviour.

Altogether, the findings of **REC** were more prevalent for the positively conditioned than for the negatively conditioned subjects and showed that reducing the input to the L hemisphere when seeing a positive stimulus entailed an increased state of attention (based on behaviour) during the object presentation, which was accompanied by a general orientation response (based on physiology). This suggests a reduced positive appraisal which would be in accordance with the emotional valence hypothesis and with previous findings showing R eye preferences for observing positive stimuli (e.g. De Latude et al., 2009; Racca et al., 2012; Rogers et al., 1994). However, most of these previous studies have shown this mainly in response to seeing food rewards or during the act of feeding, while the results in other putatively positive contexts are less clear (see Leliveld et al., 2013). Therefore, our findings in a standardized positive emotional context (achieved through conditioning) suggest that the processing of positive emotions, rather than other processes involved in responses to food, indeed predominantly take place in the L hemisphere. Note that the behavioural reaction alone would also support the approach-withdrawal hypothesis (Davidson, 1992b; Rogers & Vallortigara, 2019), since a reduced input to the L hemisphere attenuated the approach behaviour directed to the object. However, combined with the physiological reaction, our results suggest that the response is an affective, rather than a purely behavioural, response and reflects a reduced positive appraisal of the object. Monocular testing permitted us to study the role of the L hemisphere during the appraisal of a positive stimulus. Indeed, these results suggest that the L hemisphere may be important for quick recognition and evaluation of positive stimuli. Although REC first and foremost can be assumed to lead to reduced processing by the L hemisphere, we cannot fully exclude the possibility that this could also lead to increased activation of the R hemisphere as compensation. However, the investigation of this issue (by using brain imaging in human research) is still at an early stage (Wang et al., 2018). Rather, we assume that the observed reaction is more likely to be the result of reduced

L hemisphere processing than of increased R hemisphere processing. These findings shed new light on positive emotions, which are still considered difficult to assess since authors often emphasize the lack of measurable reactions (e.g. Bellegarde et al., 2017; Smith et al., 2016). Note, however, that the significant differences between the treatments in behavioural and physiological reactions in this study were numerically small compared to other studies that investigated emotional appraisal (e.g. Désiré et al., 2004; Krause et al., 2017). However, the differences found within the conditioning group were expected to be subtle, since these differences were supposed to depend not on the nature of the stimulus but on how the stimulus was perceived (Pourtois et al., 2013).

LEC (reduced input to the R hemisphere) after **positive conditioning** did not lead to significant differences from BIN (control) during the object presentation. Instead, LEC influenced some parameters during the Pre minute: the RMSSD was the lowest compared to the other treatments, which may reflect, as mentioned before for the REC treatment, a reaction to social isolation or to the anticipation of the stimulus. Additionally, the duration of locomotion increased from the Pre minute to the Post minute, suggesting increased arousal and/or avoidance-related emotions during the test (Murphy et al., 2014). However, without further results, it is difficult to make a clear conclusion about the effect of reducing the input to the R hemisphere after positive conditioning.

In contrast, **LEC** had more effects on the reaction of the **negatively conditioned subjects**: it led to an increased duration of locomotion during the presentation of the object compared to the minute before, also suggesting increased arousal and/or avoidance-related emotions (Murphy et al., 2014). However, while BIN and REC led to a significant increase in the number of vocalizations during the test, which probably indicates an increase in arousal and/or anxiety (Manteuffel et al., 2004; Murphy et al., 2014), LEC systematically led to more vocalizations than BIN, indicating higher anxiety and/or arousal independent of the object presentation. The results do not suggest an attenuation of the negative perception of the object when the input to the R hemisphere is reduced. This does not indicate a specialization of the R hemisphere in processing negative emotions as predicted by the emotional valence hypothesis. Therefore, our findings seem to contradict this hypothesis. However, without further evidence it is difficult to draw a clear conclusion. Our results thereby are not in line with previous findings of a R hemisphere specialization for processing intense negative emotions (Hook-Costigan & Rogers, 1998; Siniscalchi et al., 2008) and cannot provide clear support for the emotional valence hypothesis with regard to negative emotions.

Overall, covering the R eye caused more effects in the positively conditioned subjects than covering the L eye in the negatively conditioned subjects. This may be explained either by the fact that domestic pigs show a stronger lateralized processing of positive emotions or that the negative emotions were not as strong as the positive emotions. Because domestic pigs show particular resilience to acute stressors (Foury et al., 2007; Sutherland et al., 2006), the latter explanation seems to be more probable: the negative reinforcer may not have been equivalent to the positive reinforcer. Although the punishment used was found to be reliable (Douglas et al., 2012; Düpjan et al., 2017), it was probably not equivalent to life-threatening stimuli used in other laterality studies (Koboroff et al., 2008; Siniscalchi et al., 2010). Another explanation could be that the negative conditioning was less effective because the appearance of the object may have had

little additional effect in an already somewhat negative situation caused by inevitable testing in isolation. Since laterality is suggested to improve brain efficiency (Güntürkün & Ocklenburg, 2017; Rogers et al., 2004; Vallortigara & Rogers, 2005), it is possible that the more subtle emotional reactions of the negatively conditioned subjects were less in need of brain efficiency than the more intense emotional reactions of the positively conditioned subjects.

Conclusions

In this study, we have provided evidence of differential involvement of the two hemispheres in the visual processing of objects of opposing emotional valence. Our findings provide partial support for the emotional valence hypothesis because reducing the input to the left hemisphere seemed to attenuate the positive appraisal of a positively conditioned object. Monocular testing permitted us to provide new insight by suggesting that the left hemisphere plays a crucial role in the quick recognition and evaluation of positive stimuli. These findings demonstrate that investigating the lateralized processing of emotions can provide insight into the mechanisms of positive appraisal in animals. In contrast to positive conditioning, the results concerning negative conditioning were less clear, which was probably due to the mild nature of the stimulus. The results of this study have shown the importance of the left hemisphere in the initial recognition of positive stimuli. Therefore, an appropriate next step would be to investigate the role of each hemisphere in the long-term moods of animals to improve their welfare.

Conflict of interest

None.

Acknowledgments

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Supplementary data

Supplementary data to this article can be found online at
doi:10.1016/j.anbehav.2019.06.021

Appendix

Concerning the object-related parameters within BIN (binocular viewing, Figure 2.17), the positively conditioned subjects showed a shorter latency to touch the object (t_{129} = 5.68, P_{Tukey} <0.001), a longer duration of touching the object (t_{148} = -2.35, P_{Tukey} = 0.020) and more touches (t_{236} = -2.43, P_{Tukey} = 0.016) than the negatively conditioned subjects. Additionally, the negatively conditioned subjects showed a longer latency to vocalize (t_{124} = 2.13, P_{Tukey} = 0.036) after the introduction of the object.

The interactions between minute and condition within BIN (when viewing with both eyes) for all parameters are shown in Table 2.7. Within the Pre minute, the positively conditioned subjects vocalized more (t_{123} = -2.13, P_{Tukey} = 0.034) than the negatively conditioned subjects. Within the Post minute, the positively conditioned subjects showed a lower RMSSD (t_{183} = 4.44, P_{Tukey} <0.001) than the negatively conditioned subjects.

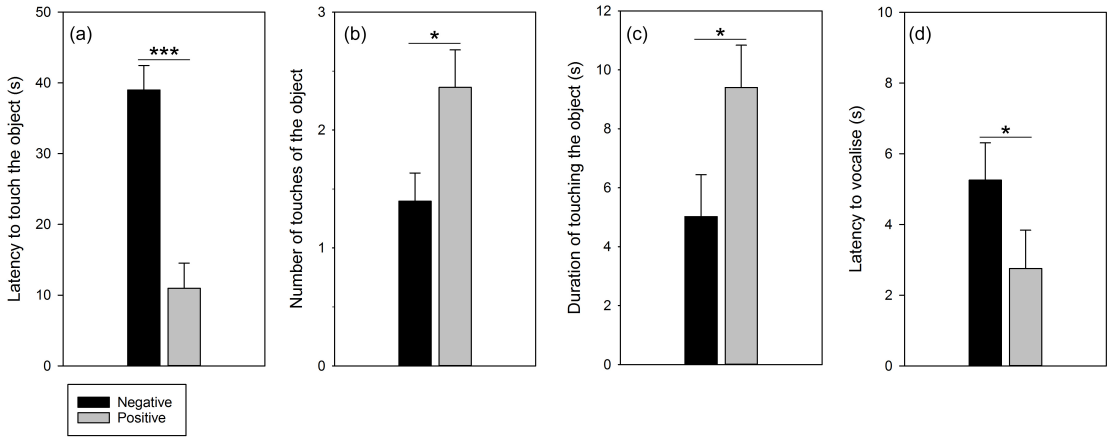

Figure 2.17: Least square means and SEs of (a) the latency to touch, (b) number of touches, (c) duration of touching the object and (d) latency to vocalize after the introduction of the object when binocular viewing according to the conditioning group. Black bars: negatively conditioned; grey bars: positively conditioned. ***P_{Tukey} <0.001; *P_{Tukey} <0.01.

Table 2.7: Behavioural and physiological responses when binocular viewing by conditioning group and minute.

Parameter	Minute	Positive	Negative
Number of vocalizations	Pre	**41.84 ± 5.40**^{a}	**31.47 ± 5.37**^{b}
	Object	42.61 ± 5.32	36.73 ± 5.29
	Post	46.57 ± 5.20	39.86 ± 5.17
Duration of exploring the arena (s)	Pre	6.88 ± 1.32	4.44 ± 1.31
	Object	4.89 ± 1.04	3.54 ± 1.03
	Post	3.29 ± 1.07	4.83 ± 1.05
Duration of locomotion (s)	Pre	31.01 ± 1.87	30.38 ± 1.85
	Object	32.48 ± 1.85	32.96 ± 1.83
	Post	32.30 ± 1.71	30.73 ± 1.69
Heart rate (bpm)	Pre	183.64 ± 6.82	167.62 ± 6.42
	Object	182.84 ± 7.45	168.83 ± 7.04
	Post	185.81 ± 9.44	163.61 ± 8.21
RMSSD (ms)	Pre	16.98 ± 1.17	20.12 ± 1.21
	Object	15.63 ± 1.27	18.66 ± 1.29
	Post	**14.03 ± 1.05**^{a}	**19.76 ± 1.12**^{b}
RMSSD:SDNN	Pre	0.71 ± 0.04	0.70 ± 0.04
	Object	0.70 ± 0.03	0.67 ± 0.03
	Post	0.63 ± 0.03	0.64 ± 0.03

Least square means are shown ± SEs. Minute: before (Pre), during (Object) and after (Post) the object was presented. RMSSD: root mean square of successive differences between interbeat intervals; SDNN: standard deviation of the interbeat intervals. The lowercase letters indicate differences between the conditioning groups within a minute. The significant differences (P_{Tukey}<0.05) are in bold.

"On n'a pas deux coeurs, l'un pour l'homme, l'autre pour l'animal. On a du coeur ou on n'en a pas."

Alphonse de Lamartine (1790-1869)

3

General Discussion

Nowadays, approaches to improving welfare have shifted focus towards quality of life in farm animals (McMillan, 2000; Webb et al., 2018; Yeates, 2016). Research on personality and emotions is considered to be crucial to this new concept because acknowledging personality and promoting positive affective states should substantially help to improve the living conditions of farm animals.

The aim of this thesis was to show that studying behavioural lateralization can help to provide new insight for animal welfare. Indeed, studying how laterality interacts with personality and emotional valence in domestic pigs represents a promising approach for improving their welfare. In section 3.1 (page 86), I will summarize the general findings of our studies. Second, in section 3.2 (from page 87), I will explain to which extent our three studies contribute to research on both personality and emotions, hence answering the sub-aims (presented in Figure 1.3, page 31) and the study-specific hypotheses of this thesis (presented in Figure 1.4, page 33). Third, in section 3.3 (from page 94), I will present the potential consequences of those studies for animal welfare with concrete examples, hence answering the general aim of this thesis (presented in Figure 1.3). Finally, after having proposed some improvements of our studies (section 3.4, from page 101), I will explore some potential further research questions that those studies might have opened (section 3.5, page 103).

3.1 Summary of the results

For the first time, our studies suggest the existence of individual hemispheric dominance in pigs (Studies 1 and 2) and validate the existence of emotional lateralization for visually processed stimuli (Study 3). The former was reflected by individual differences in motor biases for using the snout and curling the tail that were associated with individual differences in behaviour. Indeed, with the first study, we found that a majority of individuals had a consistent left (L) or right (R) bias for using the snout or for curling the tail. This suggests that pigs are lateralized at the individual level for using their snout and curling their tail. The methodological novelty of the first study was to use a cluster analysis to combine two different lateralized motor functions (tail and snout). This allowed studying lateralization at the individual level in a multidimensional way. Indeed, we could identify certain pigs with consistent motor biases for snout use and tail curling (RR and LL individuals, see Figure 2.5 of Study 1, page 47). These consistent biases across motor functions can be assumed to be caused by individual hemispheric dominance in these particular subjects. Therefore both groups were expected to contain individuals with opposite hemispheric dominance (L hemispheric dominance for RR individuals and R hemispheric dominance for LL individuals). Given the results of the second study, this idea became even more plausible since both groups significantly differed in various personality traits. Moreover, these differences were in line with the approach-withdrawal hypothesis stating that the L hemisphere regulates approach behaviours while the R hemisphere regulates avoidance behaviours (see Chapter 1, section 1.3.2 from page 15; Davidson, 1992b). In particular, R biased pigs, supposed to have L individual hemispheric dominance, were bolder (they were quicker to approach a Novel Object) and more explorative (they touched a Novel Object more often) than L biased pigs.

Finally, the last study focused on visual lateralization in pigs, and as such contributed to a more complete global picture of behavioural lateralization in this species. The methodological novelty of this study was to use the paradigm of monocular viewing (reduction of the visual inputs in the contralateral hemisphere) combined with emotional conditioning. We showed that covering the R eye during the presentation of a positive object led to an interruption in vocalisations, decreased exploration of the environment, a higher latency to touch the object, and a higher vagal activity. We interpreted this reaction as an increased attentional state co-occurring with an orienting response. Therefore, we concluded that reducing the inputs to the L hemisphere reduced the positive appraisal of a positive stimulus. This suggests a L hemispheric specialization for positive stimuli and partially supports the emotional valence hypothesis: the L hemisphere processes positive emotions while the R hemisphere processes negative emotions (see Chapter 1, section 1.3.2 from page 15; Demaree et al., 2005).

Thus, these studies confirmed that the domestic pig is a good model for testing hypotheses on emotional lateralization and that studying behavioural lateralization can contribute to better understand the underlying mechanisms regulating personality and emotions.

3.2 Studying laterality gives insights into personality and emotions

Investigating neurophysiological processes involved in affective states is expected to improve our understanding of the proximate mechanisms of behavioural control (Gygax, 2017). With the help of hypotheses on emotional lateralization, we gained knowledge on possible neural mechanisms involved in appraisal (Study 3) and on possible proximate mechanisms of personality (Studies 1 and 2). Appraisal and personality are both considered as important modulators of behavioural control (Gygax, 2017).

A striking result combined from the first and second studies is that we found indications for the phenomenon of individual hemispheric dominance in pigs. Crucially, the cluster analysis (see Study 1) suggested that individuals with a L (respectively R) hemispheric dominance resulted in consistent R (respectively L) biases for both motor functions (snout and tail). It was predicted that both these categories of individuals would show qualitative differences in cerebral patterns. This was demonstrated in the second study, where we additionally found support for the approach-withdrawal hypothesis: L and R biased individuals differed in their general motivation to investigate novelty. In other words, when responding to novelty, they differed in their behavioural output; likely reflecting individual differences in the animals' "chosen want"(Gygax, 2017). We concluded that the study of multidimensional motor lateralization patterns might be a good and non-invasive alternative to fMRI to distinguish individuals with different hemispheric dominance. Interestingly, affective styles describe combined individual differences in hemispheric baseline activities and in emotional reactions. Thus, a logical next step could be to test whether individual hemispheric dominance (determined with motor biases) correlates with the phenomenon of affective styles (determined with EEG or fMRI; see arrows 1 and 3 of Figure 3.1, page 93).

Accounting for the multidimensionality of motor laterality with the help of a cluster analysis (see Study 1) did not only give insight into individual hemispheric dominance but also provided more statistical power when the associations with personality were investigated (see Study 2). Indeed, the significant effects found between personality and individual hemispheric dominance (i.e. combined motor biases) reached a sufficient level of power (due to either a larger effect size or smaller variances between both groups) compared with the ones found between personality and single motor biases. This means that using the combined classification could help increase the robustness of studies that investigate the link between laterality and personality and this should have implications for laterality research. Indeed, we demonstrated the advantages of using a multidimensional approach for studying laterality (Studies 1 and 2). In non-human animals, combining several motor lateralization biases is rare (only in non-human primates, see Anderson et al., 1996; Prieur et al., 2016; Wesley et al., 2002). Even if some authors sometimes measure several motor biases in different tasks, they often consider single motor biases as indicators of hemispheric dominance (see Chapter 1, section 1.3.4 from page 20). Moreover, when no associations between motor tasks were found, the authors often suggest differences in task complexity to explain differences of lateralization patterns between motor functions (e.g. in dogs Batt et al., 2008; Tomkins et al., 2010b; Wells et al., 2018). However, it would be interesting to

combine those motor biases to study individual differences across motor functions as we did in the first study.

In contrast, it seems that accounting for the multidimensionality of *personality* becomes more common in laterality research (in humans: Grimshaw & Wilson, 2013; cats: McDowell et al., 2016; and dogs: Barnard et al., 2017). As demonstrated in Study 2, a multi-trait assessment of personality could help going beyond the approach-withdrawal hypothesis. Pigs with opposite individual hemispheric dominance showed different personality profiles (Studies 1 and 2): individuals with a L hemispheric dominance were bolder and more explorative than individuals with a R hemispheric dominance, as predicted by the approach-withdrawal hypothesis. Moreover, pigs with a L hemispheric dominance were more sociable than pigs with a R hemispheric dominance, which is consistent with other findings (Gordon & Rogers, 2010; Vaughan et al., 2019; Westergaard et al., 2003; Westergaard et al., 2004). Sociability, as a trait, might be related to a general approach motivation (Depue & Collins, 1999). Therefore, our results on sociability may also be considered in line with the approach-withdrawal hypothesis. As stated in Chapter 1 (see section 1.3.4 from page 20), the latter (also called the motivational hypothesis: Gainotti, 2018) seems appropriate for testing stable individual emotional lateralization patterns or personality. More generally, one could consider that Studies 1 and 2 show that consistent motor biases reflect stable individual differences in motivation (Franks, 2019; Franks et al., 2014) and therefore in "wanting". Indeed, personality or affective styles reflect the propensity of how individuals react to emotional stimuli (Gygax, 2017) and could in particular influence processes involved in "wanting" such as prioritization of stimuli or decision-making. For instance, differential prioritization of gains vs. safety has been thought to explain consistent individual differences in motivation in non-human animals, where promotion-focused (i.e. prioritizing gains over safety) vs. prevention-focused (i.e. prioritizing safety over gains) individuals could be identified (in rats: Franks et al., 2012, 2014; and in cotton-top tamarins: Franks et al., 2013). In their recent review, Cornwell et al. (2014) highlighted the importance of distinguishing promotion goals (e.g. avoidance of deprivation/non-gain, approach of growth/gain) and prevention goals (e.g. avoidance of danger/loss, approach of safety/non-loss) *within* the approach-withdrawal systems in non-human animals. However, in contrast to the third study that showed a causal relationship of monocular viewing on physiology and behaviour, the results from Studies 1 and 2 are not sufficient to conclude whether a R hemispheric dominance caused more withdrawal or whether a L hemispheric dominance caused more approach behaviour. In particular, since all pigs touched the Novel Object, one possibility is that R hemispheric dominance resulted in an heightened inhibition of approach motivation rather than directly increasing withdrawal motivation *per se* (Kelley et al., 2016). This point of view is consistent with the BIS/BAS hypothesis, which focuses on individual differences in motivational systems (Gray, 1973, 1991) and which has seen regained interest from researchers on affective styles. The BIS/BAS hypothesis states that the behavioural activation system (BAS) is regulated by the L hemisphere (Coan & Allen, 2003; De Pascalis et al., 2013; Harmon-Jones & Allen, 1997) while the R hemisphere could activate either the flight-fight-freeze system (FFFS; Sutton & Davidson, 1997) or the behavioural inhibition system (BIS; Gable et al., 2018, see Chapter 1, section 1.3.2 from page 15 for more details). It is difficult to show clear parallels between the aforementioned results and ours since most of this research was based on data measured in the brain of human R handers. However, recent findings on behavioural lat-

eralization in humans show that L handers (assumed to have a R hemispheric dominance) have higher BIS scores than R handers during situations of novelty (Beaton et al., 2015; Beaton et al., 2017; Wright & Hardie, 2012; Wright et al., 2009; Wright et al., 2004; reviewed by Vaughan et al., 2019; Wright & Hardie, 2015). Similarly, when considering the behavioural parameters independently from the personality dimensions to which the pigs were assigned (Study 2), individuals with a R hemispheric dominance (L biased pigs) might be seen as more inhibited/less impulsive than individuals with a L hemispheric dominance (R biased pigs). Indeed, L biased pigs touched the Novel Object less often, approached more slowly the Novel Object, and vocalised less often during the *Open-Field Test* than R biased pigs. Additionally, considering the single motor biases, R tailed pigs producing a higher proportion of high frequency vocalizations than L biased pigs was the only significant association with enough power between tail laterality and personality. Since we interpreted this result as L tailed pigs being bolder than R tailed pigs, it contradicted the associations found with the combined classification (L biased pigs were shyer than R biased pigs, see Table 2.4 of Study 2 on page 64). However, as stated in the second study, one might interpret this result as less vocally proactive behaviour in L tailed pigs, which may match to the picture of a less impulsive/more inhibited trait associated with a L bias (or R individual hemispheric dominance). Thus, similarly to the aforementioned studies in humans, differences in BIS traits might explain the differences between R and L biased (or between R and L tailed) pigs during a novel situation, namely the *Open-Field Test* followed by the *Novel Object Test*. Indeed, the novel situation might have triggered the BIS (supposed to solve conflicts between BAS/FFFS) more intensively in L biased pigs than R biased pigs. However, one needs to remain cautious since the second study did not originally aim at testing the BIS/BAS hypothesis. Indeed, our experimental setup could not provide the answer on whether R –respectively L– individual hemispheric dominance is associated with higher –respectively lower– BIS score or a lower –respectively higher– BAS score. To test this, one would need specific behavioural tests in the species of interest that measure BAS scores and BIS scores separately. To my knowledge, there are, as of yet, no frameworks for testing BIS or BAS scores in non-human animals. A first step in this direction might consist in combining our approach with a recent paradigm that has been developed for measuring impulse control in pigs (Zebunke et al., 2018) because it might reflect their BIS activity. Interestingly, recent findings show that innovative horses with supposed higher inhibitory control were L biased in their motor and sensory laterality (with a supposed R hemispheric dominance; Esch et al., 2019). In summary, the combined results of Studies 1 and 2 showed that studying individual hemispheric dominance through the observations of individual motor biases produces new insights into the possible underlying mechanisms regulating personality. Although we investigated several dimensions of personality, it seems that only the context of novelty revealed differences between individuals of opposite hemispheric dominance. With Figure 3.1 (page 93), I suggest that the existence of affective styles in pigs combined with BIS and BAS scores should be further investigated as it has been done in humans but not yet in non-human animals.

In the third study, we demonstrated the usefulness of testing monocular viewing combined with an emotional conditioning paradigm to gain insight into emotional valence and especially into positive appraisal. Thus, this shows that laterality research would benefit from more studies using this experimental approach, especially in other ungulate species for which studies on functional laterality have been largely overlooked (Leliveld, 2019). Indeed, the results from our third

study could not have been achieved by simply observing eye preferences. Although the observation of eye preferences has the advantage of giving information on natural and self-initiated behaviour of the species, it is not always possible to reliably observe eye preferences in pigs. Moreover, this approach may be challenging in other ungulates because they can also use their binocular field (e.g. horses for positive stimuli in De Boyer Des Roches et al., 2008). In this case, it is complicated to disentangle the precise role of each hemisphere. Interestingly, Rogers (2017b) recommends using multi-modal paradigms, such as combined monocular and monaural testing. In a further study based on a similar experimental setup as the third study, we tested the effects of monaural testing on emotional reactions in pigs which should represent a good basis for further investigations in this direction (discussed in section 3.5, from page 103).

More strikingly, the third study elucidates the importance of the L hemisphere for the processing of positive emotions in pigs which represents a valuable addition to research on positive affect. Indeed, the combined behavioural indicators (i.e. interruption in vocalising, decreased exploration of the environment, higher latency to touch the object) led us to interpret those results as a heightened attentional state (Düpjan et al., 2011) that was accompanied by a physiological orienting response (increased vagal activity: Désiré et al., 2004). In contrast to other studies on visual lateralization in emotional processing (discussed in Chapter 1, section 1.3.5 from page 24), we found a causal relationship: reducing the inputs into the L hemisphere reduced the positive appraisal of a positive stimulus. It is worth noting again that the interpretation of reduced positive appraisal would not have been possible without the combination of physiological and behavioural indicators (i.e. without using a componential view of emotions). The latter alone, however, would have been enough to support the approach-withdrawal hypothesis but not enough to support the emotional valence hypothesis, also called the affective hypothesis (Gainotti, 2018). Indeed, through the use of physiological indicators, we were able to demonstrate that the reaction was affective and reflected changes in appraisal and therefore in the core affect of the subjects. As expected, we showed that using monocular testing can be considered a non-invasive manipulation of the central nervous system during emotional processing. This manipulation is ideal for combining with indicators of both behaviour and also the autonomic nervous system. Now it can be worth discussing in greater detail what the role of an orienting response is. The function of orienting is to enhance stimulus perception (Sokolov et al., 2002) through physiological changes (e.g. in heart rate: Graham & Clifton, 1966; Porges, 1995). Orienting is nearly always accompanied by a shift in attention towards a motivationally significant stimulus and prepares the subject for a rapid behavioural response, such as a fight-flight response (reviewed in Nieuwenhuis et al., 2011). Because the orientation response seen in our study was accompanied by an increased attentional state, we interpreted this as a reduced positive appraisal when viewing a positive conditioned stimulus, as attention and orientation have already been demonstrated to be crucial for appraisal (Brosch et al., 2013; Scherer & Moors, 2019). However, as mentioned in the third study, the differences found with regard to the vagal activity were numerically smaller than those found in other studies (Désiré et al., 2004; Krause et al., 2017), which means that the orienting response observed in our study might have been less intense. Alternatively, this might be a manifestation of the lateralization of the autonomic nervous system (Craig, 2005; McGinley & Friedman, 2015; Wittling et al., 1998). However, since our experimental setup did not aim at testing the lateralization of the ANS, it is difficult to draw any firm conclusions re-

garding this hypothesis. In our study, reducing the visual inputs into either hemisphere elicited an orienting response, given the observed vagal activation that increased along the test in both monocular treatments (from the minute before to the minute after the test). We interpreted this as a possible impaired depth perception (Hughes, 1977) which might have disoriented the pigs. However, reducing the inputs to the L hemisphere specifically led to the strongest vagal activity in general (i.e. the strongest orienting response) compared with all other treatments. Interestingly, the orienting response might have been regulated by the BIS. Indeed, the BIS intervenes during goal conflicts in general by activating attention and arousal for interpreting ongoing actions (Gray & McNaughton, 2000) and this idea has been validated with EEG studies in humans (reviewed in De Pascalis et al., 2013). Thus, when the BIS is activated, one should typically observe a behaviour of "defensive approach", even in a rewarding situation (Corr, 2009), which may have been the case in our third study. Moreover, the L hemisphere has been described as playing an inhibitory control of the flight-fight response (Robins et al., 2018). Therefore, covering the R eye might have resulted in a reduction of the L hemisphere's inhibitory control (of an orienting response) which could have amplified BIS activity. It is important to note again that those motivational systems (BIS, BAS) have been conceptualized in a context to explain stable differences over time and situations in behaviour and neurophysiology (reinforcement sensitivity theory (RST) of personality, see Chapter 1, section 1.2.1 from page 5, Gray & McNaughton, 2000). Interestingly, some findings in humans show interactions between BIS or BAS traits and individual appraisal of emotions: individuals with high BAS traits experience higher R hemispheric activity for positive emotions while individuals with high BIS traits experience higher L hemispheric activity for negative emotions (Balconi et al., 2015; Balconi & Mazza, 2010). Likewise, it might be very fruitful in the future to study interactions between affective styles and the lateralized neural circuits of appraisal in non-human animals and especially in farm animals (see arrow 4 of Figure 3.1, page 93).

Our studies aimed at investigating the distinct associations either between laterality and personality (Studies 1 and 2), or between laterality and emotions (Study 3). However, throughout this thesis (and as mentioned in the previous paragraph), it became apparent that studying laterality might give insight into the associations *between personality and emotions* as well. Using the frameworks of the RST and of the BIS/BAS hypothesis in non-human animals could be promising to investigate this missing link since it could give insight into how affective styles influence individual appraisal (see arrow 4 of Figure 3.1, page 93). Moreover, this would help combine the study of motivation with core affect. This should result in a better understanding of which goals are expected in animals and therefore how they feel at the end of the process of decision-making ("liking" if the goal has been reached, "disliking" if the goal has not been reached: Gygax, 2017). A possible first step in this direction could be to study individual appraisal in non-human animals and the following speculation is based on our studies. In fact, the behavioural reaction of the pigs with an "artificial" R hemispheric dominance (achieved through covering the R eye) for seeing a positive object observed in the third study looked very similar to the reaction of the pigs with a "natural" R hemispheric dominance (reflected by consistent L biases across motor functions) towards a Novel Object observed in the second study. Indeed, in both cases, the subjects with an "artificial" or "natural" R hemispheric dominance approached the object more cautiously (longer latencies) with a reduced vocal activity (less vocalisations in Study 2, long in-

terruption of vocalising in Study 3) than the pigs with an artificial or "natural" L hemispheric dominance. It would be logical to assume that those behavioural reactions were underpinned by similar neurophysiological reactions that took place in the R hemisphere. A potential structural candidate might be the BIS as explained in the previous paragraphs. Indeed, the inhibitory activity of the BIS in pigs might have been detectable when the R hemisphere might have been dominant, either during the individual novelty tests (Study 2) or during the appraisal of a positive stimulus (Study 3). Considering the results of Studies 2 and 3 together may provide more insight into individual appraisal:

- in Study 2, if we had measured the heart rate variability of the L biased (with a "natural" R hemispheric dominance) pigs during the *Open-Field* and *Novel Object tests*, we may have observed a stronger orienting and attention response in general or at least directed to the Novel Object (according to the findings from Study 3)
- in Study 3, we could have tested whether the R eye covered pigs (with an "artificial" R hemispheric dominance) would have also shown more behavioural inhibition when confronted to novelty (according to the findings from Study 2 and to the BIS/BAS hypothesis).

As mentioned in Chapter 1, the predictions of the approach-withdrawal (motivational) hypothesis slightly differ from those of the emotional valence (affective) hypothesis. We did not aim to testing between both of these hypotheses. Instead we chose the most appropriate hypothesis for each study: the motivational hypothesis seems to be best suited for linking stable motor lateralization patterns with stable motivational traits (see Chapter 1, section 1.3.4 from page 20), while the affective hypothesis seems to be best suited for studying the link between behavioural lateralization and appraisal (see Chapter 1, section 1.3.5 from page 24). However, a necessary next step is to discover in which hemisphere the processing of aggression is situated in pigs, since both hypotheses fundamentally diverge on this point (see Chapter 1, section 1.3.2 from page 15; for further emotions, see Kelley et al., 2016).

In general, all those studies combined show that studying laterality allows not only for the non-invasive elucidation of the mechanisms of positive appraisal, but also the identification of individuals with different cerebral organizations and whether those individuals differ in their appraisal according to which hemisphere they "prefer" to use.

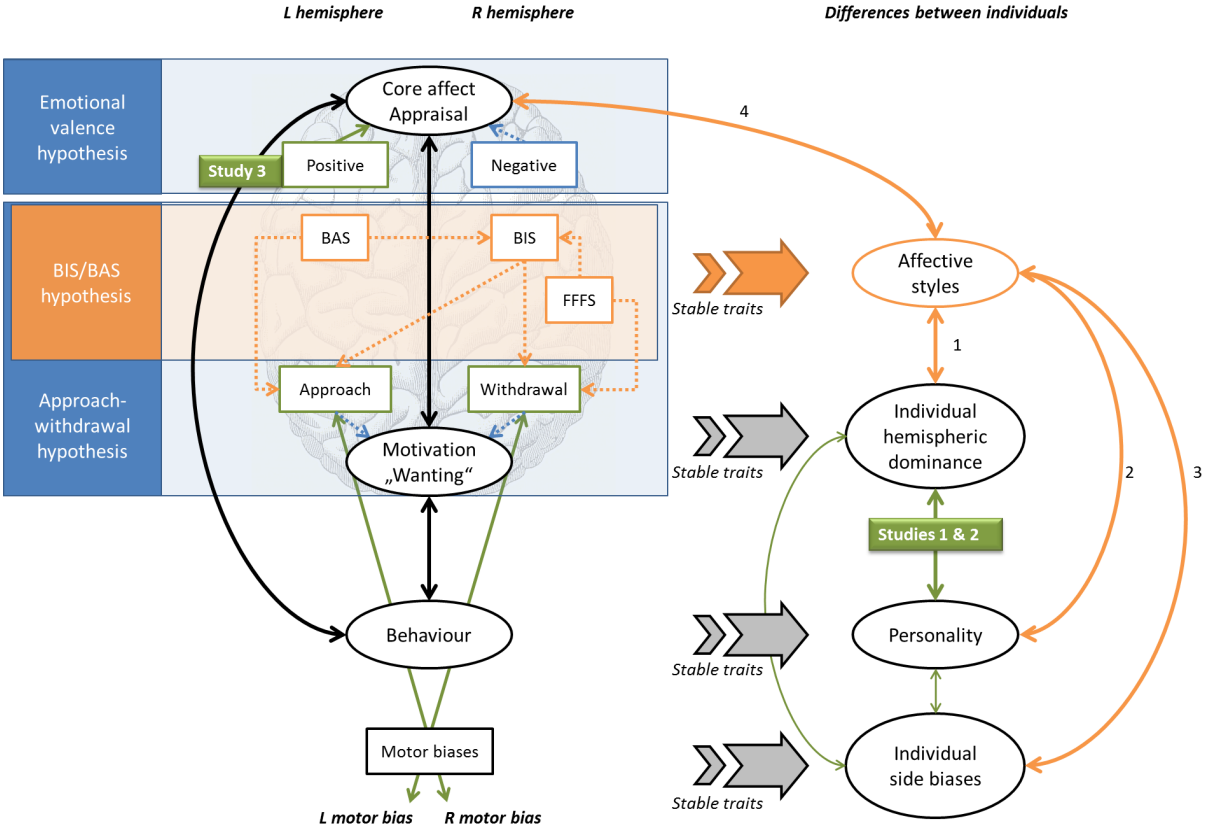

Figure 3.1: *Suggestions for further research directions (in orange) according to the results presented in this thesis (in green) and based on Figure 1.4, page 33*

Solid lines represent the links between the core concepts of this thesis (in oval shapes), presented in Figure 1.1, page 13. Big right pointing arrows illustrate that stable traits in e.g. behaviour or affect result in the emergence of personality or affective styles (explained in Figure 1.1). Dotted lines link the predictions of each hypothesis (in rectangular shapes) to each proposed core concepts of this thesis (explained in Figure 1.2, page 17). Green solid lines show the confirmed hypotheses of each study (presented in Figure 1.4). Green double directed lines illustrate associations while the green one-directed line illustrates a causal link. The combined Studies 1 and 2 supported the approach-withdrawal hypothesis and allowed to conclude a link between individual hemispheric dominance and personality. Study 3 partly supported the emotional valence hypothesis since it validated a left (L) hemispheric specialization for processing positive stimuli and especially for positive appraisal. Future research might benefit from investigating the existence of affective styles in non-human animals (discussed in text) which should intimately correlate with the concept of individual hemispheric dominance (1). Similarly to human research, developing methods that measure individual differences in behavioural activation (BAS) and behavioural inhibition (BIS) systems and being able to test the BIS/BAS hypothesis in non-human animals should be promising. In pigs, a first step could be to test whether both personality (2) and individual side biases (3) are associated with measurements of cerebral baseline asymmetries (see text for more details). Furthermore, the study of affective styles might help explaining individual appraisal (4).

3.3 Studying laterality has implications for animal welfare

Our studies report the presence of emotional lateralization in pigs. Not only do these studies contribute to research on personality and emotions (i.e. sub-aims presented in Figure 1.3, page 31), they also have implications for animal welfare (i.e. general aim presented in Figure 1.3, page 31). This section will mostly demonstrate that studying specific features of laterality in pigs (strength vs. direction, biases at the population vs. individual level) can have direct and indirect implications for their welfare. Indeed, as stated in Chapter 1, individual behavioural lateralization patterns can differ in strength or direction and might reflect similar mechanisms regulating personality (explained in Chapter 1, section 1.3.3 from page 18). For this reason, similarly to the study of personality, the study of laterality at the individual level could show similar potential benefits (similarly to those presented in Chapter 1, section 1.3.6 from page 26), in particular for individualized care or group management. Additionally, laterality at the population level can sometimes emerge and is thought to facilitate group coordination (explained in Chapter 1, section 1.3.3) which is relevant for the study of social (intra- and interspecific) interactions (explained in section 1.3.6). Therefore, studying laterality at the population level can be also helpful in group management and handling practices. Moreover, the study of laterality at the population/group level can improve the understanding of the species of interest which may give insight into "micro-behaviours" and enable us to access the "animal's point of view" during a specific situation (see also Chapter 1, section 1.3.6). Our studies support the existence of emotional lateralization at the individual level (Studies 1 and 2) and at the population level (Studies 1 and 3). First, some direct applications of our combined findings for animal welfare will be mentioned. Second, the advantages of studying laterality at the individual level and their potential usefulness for improving animal welfare will be highlighted. On one hand, the classification system used in Study 2 (direction of laterality) will be presented as a potential approach for bridging research on coping styles and research on affective styles. On the other hand, I will propose to further investigate strength of laterality in the context of group management. Third, since we found a population bias for tail curling, I will state that studying the laterality of unpaired organs deserves further research in general. Indeed, the finding that tail curling is lateralized at the population level has already some consequences for pig welfare. And finally, the implications for having gained knowledge on positive appraisal for animal welfare (and well-being) will be discussed.

First of all, the most direct (and maybe obvious) application based on our findings that one can imagine is as following: despite the "unnatural" housing conditions in which they are reared, intensively farmed pigs should have the freedom to express their individual side preferences. Our first study suggests that pigs probably show individual side preferences during rooting with their snout. Thus, providing a variety of physical enrichments should allow them to satisfy their individual needs for "lateralized foraging". Our third study shows that not only the subject's individual hemispheric dominance but also the situation can predetermine eye preference. Indeed, pigs should be allowed to choose with which eye they look for a specific stimulus, according to how they perceive it. This behavioural need cannot be fulfilled in animals with restricted space use, such as the individually-housed sows (in the mating unit or farrowing crates) which are pre-

vented from turning around (Pedersen, 2018) and which goes against the recommendations of the Brambell committee (see Chapter 1, section 1.1.2 from page 2; Brambell Committee Report, 1965). Even if sows can express their lying side preferences during nursing in their farrowing crates (Illmann et al., 2002), our studies prove that behavioural laterality is multidimensional, involving several motor and sensory functions. A lying preference might be predetermined by several motor and sensory preferences, but reduced space allowance might force the animals to reduce the expression of these preferences. Therefore, with the provision of – at least – more space, sows should be able to express simultaneously their motor and sensory preferences, which belong to their natural behaviour.

As stated in Chapter 1, accounting for individual differences and especially for personality in farm animals is necessary for animal welfare research (Bushby et al., 2018; Finkemeier et al., 2018; Richter & Hintze, 2019). Understanding how farm animals experience their environment is crucial to determine their individual wants and needs (Bushby et al., 2018; Franks, 2019) and could allow for the design of environments adapted to fulfil these wants and needs, e.g. with respect to environmental enrichments (Loyer & Ha, 2017; Richter & Hintze, 2019). Studying laterality at the individual level could help distinguish individuals with different personality in pigs as has already been demonstrated in Study 2 but also in other domestic ungulates (Barnard et al., 2015; Goma et al., 2018; Hopster et al., 1998; Prelle et al., 2004; reviewed by Leliveld, 2019). As mentioned before, it would be interesting to determine how well our classification based on individual motor lateralization patterns reflects affective styles in pigs (see arrows 1 and 3 in Figure 3.1, page 93). In doing so, this classification might be used to non-invasively distinguish individuals with different affective reactions during everyday situations. Indeed, our studies suggest that our classification system reflects qualitative differences in brain structures that might underpin differences in personality. Therefore, similarly to coping, this classification is based on individual differences in both behaviour and physiology. Even if our results were in line with some indications that R biased individuals can show a more proactive coping styles than L biased individuals (Fahim et al., 2018; Phillips et al., 2015; reviewed by Rogers, 2010), we also validated the idea that it is beneficial to include a broader spectrum of personality traits (e.g. including boldness, exploration, sociability) than only coping (O'Malley et al., 2019). Indeed, in Study 2, we remained cautious with the interpretation of the link between coping (supposed to be reflected by the duration of struggling during the *Backtest*) and laterality because its power was not high and no effects on the other *Backtest* parameters (latency and frequency of struggling) could be found. Our new classification system might be a basis for answering further research questions that could be similar to those that have been answered in respect to coping: how coping style influences affective reactions that are relevant to everyday life (Krause et al., 2017), how coping style interacts with environment (Bolhuis et al., 2005a), how coping interacts with other personality traits (Bolhuis et al., 2005b) or with behavioural flexibility (Bolhuis et al., 2004), and how the study of coping can be used to improve group management (Ruis et al., 2001; Ruis et al., 2002). Two main advantages of the classification system based on motor lateralization in comparison to the framework of coping are that the behavioural testing is less invasive and less demanding (i.e. in pigs: observing motor lateralization patterns instead of performing the *Backtest*), and that one seems to obtain a more complex (and therefore more realistic) overview of the population (LL, RR, LR, RL or more categories if more motor functions are included; instead of reactive,

proactive, intermediate). Using this classification might help switching from the framework of coping (as recommended by O'Malley et al., 2019) and classifying pigs based on their affective styles (emotional reactivity in the everyday life) rather than on their coping styles (reaction during stress).

Additionally, it seems that studying the strength of laterality might give insight into possible trade-offs between different personality traits. According to the distribution of the laterality indices, it is worth noting that using the snout for reaching a reward elicited more individual variability in strength compared to tail curling. Therefore, in Study 2 snout use was an appropriate motor function to also test the associations between strength of laterality and personality. In line with other findings (Branson & Rogers, 2006; McDowell et al., 2016; Reddon & Hurd, 2009b), strongly lateralized pigs were interpreted as bolder than weakly lateralized pigs, because strongly lateralized pigs produced fewer high frequency calls than weakly lateralized pigs. Additionally, weakly lateralized pigs were more explorative (they explored the Open Field longer) than strongly lateralized pigs, which to my knowledge represents a novel finding. Indeed, there are no classical hypotheses on emotional lateralization predicting links between strength of laterality and personality. Instead, strong laterality is often argued as being advantageous (Rogers, 2017a), although recent findings show that it might also reduce fitness (Frasnelli & Vallortigara, 2018; Leaver et al., 2020; Whiteside et al., 2018). In fact, strength of laterality is seen as promising for studying trade-off mechanisms between opposite types of behavioural strategies (Frasnelli & Vallortigara, 2018). A concrete illustration of this could be the recent findings showing that lateralized fish escaped a predator more efficiently but were poorer competitors than non-lateralized fish (Chivers et al., 2017). In contrast, our findings combined with those of Camerlink et al. (2018a) might support the idea that strong lateralization in pigs may be advantageous for competitive situations, in terms of the ability of taking rapid decisions. Indeed, strongly lateralized pigs are bolder (Study 2) and show shorter contest durations but do not win more fights (Camerlink et al., 2018a) than weakly lateralized pigs. Camerlink et al. (2018a) already suggested that strength of lateralization might therefore reflect trade-offs between speed and accuracy during contest scenarios. Though important in the pig industry, fighting is not the only relevant behaviour for their welfare. For instance, individual differences in exploration have implications for how pigs interact with their physical enrichment (Bolhuis et al., 2006). According to our second study, weakly lateralized pigs spent more time exploring a novel environment than strongly lateralized pigs. Longer exploration might provide advantages in situations requiring accuracy in decision-making rather than in competitive situations (Sih & Del Giudice, 2012). This interpretation would partly fit the prediction of Camerlink et al. (2018a): strongly lateralized pigs might show a rapid decision-making style while weakly lateralized pigs might have an accurate decision-making style. These findings appear similar to previous findings showing that low reactive pigs explore longer their environment than high reactive pigs (Hessing et al., 1994; Ruis et al., 2000; Zebunke et al., 2017). However, strength of laterality did not show associations with any *Backtest* parameter. Our second study combined with the study of Camerlink et al. (2018a) might represent a first step for studying trade-offs in strength of laterality in the context of animal husbandry. A next step could be to investigate groups with different proportions of weakly vs. strongly lateralized pigs and test how they differ in level of aggression or stress. Again considering research on coping style, Ruis et al. (2002) studied how the interac-

tions between dominance status and coping styles influenced the welfare of pair-housed gilts. The authors found out that the combination of low reactive dominant with high reactive submissive gilts resulted in the lowest level of stress. Similarly, studying the interactions between strength of laterality and personality at the group level could help to determine which balance of weakly vs. strongly lateralized individuals is optimal for managing group of pigs.

Our first and second studies demonstrate that investigating motor laterality gave new insight into the species of interest. In particular, we found that investigating motor laterality of unpaired organs in pigs deserve further investigation in general (snout and tail). Indeed, our results showing individual motor lateralization for tail and snout was in line with the findings from the rare previous studies of other unpaired organs, such as tails in other species (rats: Denenberg et al., 1982; new world monkeys: Laska, 1998; Laska & Tutsch, 2000; dogs: Quaranta et al., 2007), elephant trunk (Martin & Niemitz, 2003), primate mouth (Wallez & Vauclair, 2012) or cat tongue (Reiss & Reiss, 2002). This could generate curiosity among behavioural biologists and lead to further investigations on unpaired organs in other species (e.g. tail in ungulates). Indeed, in her review on laterality research in ungulates, Leliveld (2019) reported only four articles (from a pool of 132 articles) that investigated tail postures and their potential lateralization patterns (Goma et al., 2018; Lane & Phillips, 2004; Phillips et al., 2003; Reefmann et al., 2009a). Given the potential role of tail postures in micro-behaviours, there is a need for more investigating this motor function (Camerlink, 2019). The study of micro-behaviours might help understanding how animals naturally express their intents (Camerlink, 2019; Camerlink et al., 2018b) and therefore might help predicting their wants. To my knowledge, the second study represents the first findings linking lateralization of unpaired organs with personality (but see Cox et al., 2018) which is one aspect of emotional lateralization. Further investigations on additional motor tasks in which pig's snout and tail might be involved could help to understand better their function. For example, it would be interesting to know whether those motor biases can also reflect emotional reactions of different valences. Can the snout also show lateralized patterns during specific emotions and be therefore used as an indicator of facial expressions in pigs (as it has been shown for primate mouth: Wallez & Vauclair, 2012)? Can the tail show other lateralized postures during specific emotional reactions (similar to wagging in dogs: Quaranta et al., 2007)? In particular, although tail function remains unknown in pigs, tail movements and postures have been shown to reflect pain (Hay et al., 2003; Noonan et al., 1994) and more subtle emotional reactions (Marcet Rius et al., 2018; Reimert et al., 2014, 2013; Reimert et al., 2017). The next step could be to study the lateralization of those postures/movements because it could even reflect pigs' motivation to approach or withdraw a stimulus, as it has been shown in dogs (Quaranta et al., 2007). With our first study, we demonstrated that the "simple" observation and description of spontaneous lateralized tail curling gave insight into its function and may be a promising tool for the better understanding of pigs. Indeed, we surprisingly found that tail curling was lateralized at the population level: a majority of individuals showed a R tail bias (see Study 1). This suggests that it might play a function in social coordination (Vallortigara & Rogers, 2005). However, it is important to investigate whether this tail asymmetry is not simply a directional (morphological) asymmetry, such as the heart position in mammals (Palmer, 2004). Initial analyses are currently running concerning the muscular asymmetries of pigs' tail which could help understanding the dynamics of tail curling. Another unexpected result was that tail curling (a posture) was also more strongly

lateralized than snout use (an "active" behaviour). According to the task complexity hypothesis, this indicates that tail curling might be more complex than snout use (Fagot & Vauclair, 1991). In the first study, we discussed different possible origins which could have led to this R population bias. In short, tail curling is not present in wild boars (Jensen, 2002) and can be seen as a morphological marker of the domestication process (Trut, 1999; Trut et al., 2009). Therefore, the R population bias of this behaviour might have resulted from an increased selection of individuals with L hemispheric dominance resulting in more approach behaviours towards humans (according to the approach-withdrawal hypothesis). However, individuals with opposite tail biases did not differ in their response during the *Human Approach Test* (see Study 2), thus we could not validate this hypothesis. The absence of results might be due to the use of group testing (discussed in Study 2), therefore it might be interesting in the future to test whether R tailed pigs approach more humans in individual conditions. If this is true, this would have implications for handling practices (discussed in the next paragraph). Alternatively (but not exclusively), tail movements can play a communicative role (Kiley-Worthington, 1976). For example, Cafazzo and Natoli (2009) found that domestic cats lift their tail more often than wild cats, as a result of increased sociability and thus of increased need of communication with conspecifics and humans. Moreover, since communication is a L hemispheric specialization (Ocklenburg et al., 2013), the R population bias for tail curling might reflect a L hemispheric dominance resulting from an increased need of communication in domestic pigs. This idea might be supported by the findings of Study 2 since we could distinguish individuals with different tail biases based on their vocalisations: individuals with a R tail bias were more vocally active than individuals with a L tail bias. For all these reasons, behavioural lateralization of tail in pigs deserves further investigations since it might help not only the understanding of tail function but also improve pig's welfare. In particular, there should be implications for the common practice of tail docking in pig's production despite its prohibition by the EU (Dippel & Schrader, 2016; Valros & Heinonen, 2015). Indeed, tail docking is believed to reduce the incidence of tail biting (Valros, 2018). The latter is a maladaptive behaviour that can appear with intensive husbandry (Done, 2011; Feddes & Fraser, 1994; McGlone et al., 1990; Statham et al., 2009). Tail biting is still considered as the most serious behaviour problem in modern pig production systems (Chou et al., 2019; Prunier et al., 2020; Valros, 2018). Regulations from the EU prohibit routine tail docking, however they allow it if no other methods have been successful in reducing tail biting outcomes. As a consequence, 90% of European pigs are docked (Valros, 2018). This is a major welfare issue since it causes acute and chronic pain and therefore it has been abolished in some countries, such as Switzerland, Sweden, Norway and Finland (Valros, 2018). More subtly, the results of our first study suggest that the direction of tail curling might play a role in coordination or communication; therefore tail docking might also impair pig's social life or at least the signalling of their micro-behaviours. If dogs interpret communicative cues less successfully when seeing docked tails of conspecifics (Artelle et al., 2011; Leaver & Reimchen, 2008), why should it be so different in pigs? Due to its practical aspect (non-invasiveness, quick and easy to observe), studying laterality seems to be an ideal approach for more interdisciplinary work between fundamental and applied behavioural research in farm animals, which is necessary to improve their welfare. For example, based on our first study and on previous findings indicating that tail posture can predict tail damages related to tail biting (Zonderland et al., 2009), the first applied studies on the

motor lateralization of tail curling are appearing. Preliminary results seem to indicate that pigs with a weaker tail bias tended to show higher tail lesion scores due to tail biting (Chou, personal communication). If those results are validated, it would be a direct demonstration of the usefulness of investigating tail laterality in pigs since it could help identify individuals that would need individualized care. Thus, our studies demonstrated that investigating tail laterality allow us to acknowledge the importance of keeping (rather than docking) the tails in pigs while observing tail curling behaviour may help investigating solutions for getting rid of tail biting in pig industry.

In general, the first study alone demonstrated that studying behavioural lateralization at the population level (in our case, of tail curling) has unique potential for understanding human-animal interactions and to a further extent domestication mechanisms. This issue is also relevant for animal welfare because it is important to understand the behavioural needs of domestic animals regarding their relationship with humans. On the one hand, one could get insight into how farm animals approach humans. For example, a new hypothesis based on our findings on tail curling (see the previous paragraph) could be tested in pigs: do R tailed pigs show an increased general motivation to approach (and even communicate) with a human compared with L tailed pigs? On the other hand, the study of laterality can give insight into how we should approach farm animals. For example, findings in cattle (Goma et al., 2018; Phillips et al., 2015; Robins et al., 2018) or in horses (Farmer et al., 2010; Larose et al., 2006; Schuetz et al., 2017) interacting with humans could be used to determine from which side to approach and handle animals. Therefore, comparing lateralization patterns at the population level between domestic, feral and wild species might be helpful to understand how human selection influenced certain behavioural traits. For instance, on the one hand, Przewalski horses show stronger patterns of visual lateralization compared to domestic or feral horses (Austin & Rogers, 2012, 2014), which might be due to a decreased need of group coordination for non-wild species. Indeed, domestication process can result in a reduced group synchronization as an adaptive response to captivity (Eklund & Jensen, 2011). On the other hand, Austin and Rogers (2012) showed that feral horses do not show limb preferences at the population level in contrast to their domestic counterparts, suggesting a substantial influence of human training on motor lateralization in horse. Thus, if the study of laterality can improve understanding of domestication processes, it may also facilitate the challenging integration of farm animal behaviour (and therefore of welfare-relevant traits) into breeding goals (e.g. selection against aggressiveness or tail biting in pigs: Turner et al., 2018). Our third study aimed also at investigating behavioural lateralization at the population level in order to understand better how lateralized visual inputs influence emotional reactions. The findings may suggest that presenting a positive stimulus to the L eye of pigs might be perceived as less rewarding than if the same stimulus is presented to the R eye. This kind of fundamental research combined with applied studies could also have implications for research on pig-human interactions, which aims at improving handling practices so that pigs perceive humans positively (Tallet et al., 2018). For example, preliminary observations showed that a majority of pigs initially use their L eye for looking at humans who take photographs (Marchant-Forde & Marchant-Forde, 2014). Those observations combined with the findings of our third study might suggest that pigs do not perceive this situation as rewarding (maybe due to the use of flash photography).

However, the main result of the third study is that we were able to measure subtle changes in positive affect. Therefore, our findings open the door for more research using similar paradigms to monocular viewing in order to better understand the mechanisms of positive appraisal in animals. As mentioned in previous section, these kind of studies (like Study 3) could be combined with studies on individual hemispheric dominance (like Studies 1 and 2) in order to better understand individual appraisal, or affective styles in non-human animals. Moreover, appraisal and personality may both be seen as modulators of "liking" (when the goal expected is reached in the framework of behavioural control: Gygax, 2017). In Study 3, the use of emotional conditioning excluded any indicator of "liking" because the pigs were not exposed to unconditioned stimuli (i.e. an actual reward or punishment). However, one can speculate that this study might have given insight into potential modulators of the feedback system involved in "liking". For instance, with the last study we showed that reducing the input to the L hemisphere may have increased attentional state. The attention given to a stimulus might be one of several processes that help an individual to obtain information about "what is real". The "establishment of what is real" is considered as an important modulator of "liking" (Cornwell et al., 2014; Gygax, 2017). In a next step, it would be appropriate to use the paradigm of monocular viewing combined with an attentional bias test. The latter measures the relative evaluation of a positive or negative stimulus (Bar-Haim et al., 2007) and the first studies in farm animals showing interactions with anxiety (Lee et al., 2018; Lee et al., 2016) or mood (Raoult & Gygax, 2019) are promising. Studies combining interactions between emotional lateralization and attentional biases might help to understand interactions between valence, attention and salience (Brosch et al., 2013; Pourtois et al., 2013; Schepman et al., 2016) and therefore to understand how "liking" is modulated. In general, the framework offered by the hypotheses on emotional lateralization as shown in our studies is promising for understanding the mechanisms of "wanting" and of "liking" to a better extent, a consideration which should be predominant in new research questions involved in animal well-being (Franks, 2019; Gygax, 2017).

To conclude this section, all three studies provided new insight into behavioural lateralization in pigs at the individual as well as at the population levels. This triggered potential challenging questions (e.g. function of tail curling; potential trade-offs between fighting ability, boldness and exploration; human-animal interactions; positive appraisal) that could help to better understand this species and improve animal welfare (e.g. the practice of tail docking, optimal group management, handling practices and the mechanisms of "liking" respectively).

3.4 Suggestions for methodological improvements

Further research on this topic would greatly benefit from the following suggestions to improve some aspects of our studies.

In Study 1, one might criticize the experiment for testing snout use since this setup might be compared with the ones used for testing detour behaviour (i.e. eye preferences to look at a specific stimulus when detouring an obstacle) in other species (fish: Bisazza et al., 1997; dogs: Siniscalchi et al., 2013; birds: Vallortigara et al., 1999). This would suggest that we might have measured eye preferences for looking at a positive stimulus (i.e. a food reward) instead of snout bias for opening the flap door. However, this is unlikely since the food was hidden behind the flap door. Therefore, we can conclude that the observed biases were most likely rather due to snout use than to eye preferences. Concerning foot laterality, we concluded that stepping with the foot might be not relevant in the everyday behaviour of pigs since the laterality indices for the forelimb showed normal distributions. This reflected that a majority of individuals had no consistent bias for their forefoot during the locomotor activity which is in line with findings in goats (Langbein, 2012; but see: Baruzzi et al., 2018) and sheep (Versace et al., 2007). However, digging with the forelimb has been found to be lateralized in other Artiodactyla (Espmark & Kinderås, 2002). Such tasks for using the forefoot also exist in the pig's behavioural repertoire –at least "pawing" in sows during nest building (Burne et al., 2000; Jensen, 1993). For instance, digging with the forefoot might be expected to be lateralized since this function seems also involved in foraging. An easy observation of this behaviour could be done by providing small food rewards (e.g. chocolate raisins) hidden by a straw layer on the floor (personal observation). Integrating this motor function into a cluster analysis in future studies on individual behavioural lateralization patterns might be helpful to gain insight into more accurate hemispheric dominance and possibly with more (robust) effects on personality traits, as demonstrated in Study 2. Indeed, we are well aware that the 30 selected individuals for studying the associations between personality and laterality (identified as RR and LL individuals, see Figure 2.5, page 47) did not represent a majority in our population (n=80). Instead of arguing in Study 1 that the 50 individuals with inconsistent biases for snout use and tail curling (identified as RL and LR individuals, see Figure 2.5) did not show individual hemispheric dominance, we assumed that more motor functions were needed to determine their hemispheric dominance. Therefore, I suggest studying the behavioural lateralization of digging in the future.

As aforementioned, the cluster analysis (performed in the first study and used in the second study) enabled us to identify individuals with different hemispheric dominance as well as to obtain more robust results. However, some authors recently suggested that using a latent class analysis could be "superior" to a cluster analysis to classify individuals across several lateralized functions, because cluster analyses contain arbitrary chosen distance measures between clusters (Tran et al., 2014, 2015; Tran & Voracek, 2016). This latent class analysis enabled authors to classify human sidedness using scores of handedness, footedness, "eyedness" and "earedness" (Tran et al., 2014). Most of all, this approach gave insight into the associations between the different motor and sensory functions and surprisingly showed that footedness is a better predictor of sidedness than handedness (Tran et al., 2014). However, this kind of analysis would be only

possible with a substantially heightened sample size ($N > 15{,}100$ in the study of Tran et al. (2014) vs. 80 pigs in our Studies 1 and 2).

In Study 3, since we aimed at testing lateralization for processing emotions of different valences, the scope of this study was not about testing individual eye preferences. However, owing to the results in Studies 1 and 2, one might expect to also find individual visual lateralization patterns (Hook-Costigan & Rogers, 1998). Eye preferences (e.g. for looking through a hole, like in primates studies: Hook-Costigan & Rogers, 1998) could have been a good complement to the third study since it would give insight into individual appraisal. Strikingly, in the third study, we failed at finding an effect of monocular viewing during the negative conditions. We therefore could not conclude about the role of the R hemisphere in the processing of negative emotions. We interpreted this as a possible imbalance in stimulus intensity and/or an absence of needing a lateralized response in this context. Indeed, the positive stimulus was associated with a food reward while the negative stimulus was rather associated with a mild punishment. Although this punishment has been validated in previous studies (Düpjan et al., 2017; Leliveld et al., 2017), it cannot be compared to fear of predator or aggression towards conspecifics like in other studies on emotional lateralization (e.g. Koboroff et al., 2008; Robins et al., 1998). Similarly, Gygax et al. (2013) found a L hemispheric activation when goats had access to a food reward, while no effects of lateralization were observed during a situation of frustration which can also be considered as a "mild" punishment. Thus, we could ask whether the use of "mild" negative stimuli is appropriate for laterality studies. I personally do not consider the use of "stronger" punishment as an alternative, first because of ethical reasons and second because the use of extreme stimuli has been already criticized in the study of emotional valence. Indeed extreme negative stimuli have been argued of being unrealistic for the animals (Camerlink, 2019; Gygax, 2017). Instead, I suggest combining similar approaches used in the third study (monocular viewing combined to emotional conditioning) with direct measurements of cerebral activity (such as fNIRS or EEG) during mild punishments in order to distinguish between an absence of behavioural reaction and an absence of emotional lateralization.

In general, our studies demonstrate that studying laterality is an insightful approach to investigate mechanisms occurring in the central nervous system. As (hopefully) demonstrated in this thesis, making the distinction between different hypotheses on emotional lateralization gives insight into cerebral lateralized mechanisms involved in distinct mechanisms such as "wanting", appraisal (see Figure 3.1, page 93) and potentially "liking". Thus, it helps to integrate the brain in behavioural studies without considering it as "an abstract computing machine" (Gygax, 2017). However, without fine measurements of cerebral activity, one can quickly face the limitations of this approach. For example, our studies cannot inform us about the precise location in the brain where appraisal or individual hemispheric dominance are actually measurable. Therefore, implementing our studies with fNIRS, EEG or fMRI would be fruitful in the future in order to identify which neural structures are involved in emotional lateralization.

3.5 Outlook

As mentioned in section 3.2 (from page 87), Rogers (2017b) recommends future research on lateralization that should integrate different sensory modalities in order to better understand how the lateralized neural circuits interact. In pigs, the logical next step would be to investigate the lateralization of audition and olfaction. As mentioned before, in a fourth study we tested the effects of monaural hearing on emotional reactions by using the same experimental paradigm as in our last study. In the future, this should facilitate the designing of experiments combining monocular and monaural testing in pigs, as recommended by Rogers (2017b). Olfaction is also known to be very relevant in pigs and it would be interesting to explore this modality using similar approaches as in Study 1 or Study 3 in order to gain insight into emotional lateralization patterns. Therefore, we also studied nostril biases in pigs, because it might help understanding the role of olfactory cues in emotional appraisal (Siniscalchi, 2017).

Throughout this thesis, I regularly referred to the concept of affective styles because their study could be promising for understanding the interactions between affective states (i.e. emotions and moods) and personality. As discussed in section 3.2 (from page 87), our three studies together might represent a first step in this direction. A next step would be to use brain imaging techniques to enable measurements of baseline activity in each hemisphere. Those measurements could be expected to correlate with indicators of individual hemispheric dominance (as found in Study 1, see arrows 1 and 3 of Figure 3.1, page 93) and with indicators of personality (similarly to Study 2, see arrow 2 of Figure 3.1) or mood (as found in Gordon & Rogers, 2015; Marr et al., 2018; Wells et al., 2017). Moreover, affective styles might also predetermine individual appraisal (see arrow 4 of Figure 3.1) and to a further extent they might predict individual differences in "liking".

Finally, as mentioned in section 3.3 (from page 94), an interesting perspective would be to evaluate how brain lateralization has been influenced by domestication processes. It has been shown that brain size is reduced in domestic animals compared with their wild counterparts (Kruska, 1980, 1988, 2005). However they do not necessarily show lower cognitive abilities (Kruska, 2005; Nawroth et al., 2019). What if the brain of domestic animals may be more lateralized, implying more efficient neural circuits? Comparative studies on the corpus callosum –responsible for the connection between both hemispheres– might help answering this question (Karolis et al., 2018; Spocter et al., 2018).

3.6 Conclusion

To conclude, it appears nowadays difficult to overlook the phenomenon of laterality in behavioural studies investigating internal states. Thus, this thesis supports the idea that using theory-driven studies on emotional lateralization can help in advancing animal welfare research. The first study showed that pigs could be distinguished in their potential individual hemispheric dominance by investigating individual lateralization patterns of various motor functions. The second study showed that pigs with distinct hemispheric dominance differed in their personality which gives insight into their individual emotional processing. Since both studies accounted for multidimensionality of motor laterality and personality, they helped in comprehending individuality in animals: a major challenge in animal welfare science. The new classification based on individual motor biases of snout use and tail curling reflects qualitative differences in brain structures that are supposed to be at the origin of differences in personality. More generally, this might reflect distinct affective styles in pigs, a concept that has not yet been investigated in non-human animals. Further investigation in this direction should be promising for the understanding of the individual needs and wants of farm animals. The third study aimed at directly testing hemispheric specializations for emotional valence using a paradigm of monocular presentation of emotional conditioned stimuli. We showed that this setup is a valuable addition to the componential view of emotions since it amounts to a non-invasive manipulation of the central nervous system. This study improved our understanding of positive appraisal (regulated by the L hemisphere) in pigs which also represents a major challenge in the modern view on welfare: the focus on a life worth living in farm animals. Direct implications for pig welfare of those studies should be to keep the pig's tail (e.g. banishing tail docking) and to offer more space (e.g. avoiding individual crates) to pigs so that they are free to express their individual side preferences. Finally, those studies contribute to gain more insight into the proximate level of behavioural control and should encourage further interdisciplinary research on emotional lateralization in farm animals by for instance combining neurosciences with applied studies.

References

Abbey-lee, R. N., Uhrig, E. J., Garnham, L., Lundgren, K., Child, S., & Løvlie, H. (2018). Experimental manipulation of monoamine levels alters personality in crickets. *Scientific Reports*, *8*, 1–7. doi:10.1038/s41598-018-34519-z

Ahern, G. L., & Schwartz, G. E. (1979). Differential lateralization for positive versus negative emotion. *Neuropsychologia*, *17*, 693–698. doi:10.1016/0028-3932(79)90045-9

Alcock, J. (2003). A textbook history of animal behaviour. *Animal Behaviour*, *65*, 3–10. doi:10.1006/anbe.2002.2044

Allen, T. A., & DeYoung, C. G. (2016). Personality neuroscience and the five factor model. In A. W. Thomas (Ed.), *The Oxford handbook of the five factor model of personality* (Vol. 1, pp. 319–352). New York, NY: Oxford University Press.

Amills, M., Clop, A., Ramírez, O., & Pérez-Enciso, M. (2010). Origin and genetic diversity of pig breeds. *Encyclopedia of Life Sciences*, 1–10. doi:10.1002/9780470015902.a0022884

Anderson, J. R., Degiorgio, C., Lamarque, C., & Fagot, J. (1996). A multi-task assessment of hand lateralization in capuchin monkeys (*Cebus apella*). *Primates*, *37*, 97–103. doi:10.1007/BF02382926

Anderson, M. J., Williams, S. A., & Bono, A. J. (2010). Preferred neck-resting position predicts aggression in Caribbean flamingos (*Phoenicopterus ruber*). *Laterality: Asymmetries of Body, Brain and Cognition*, *15*, 629–38. doi:10.1080/13576500903081814

Andics, A., Gácsi, M., Miklósi, Á., Szabó, D., Faragó, T., & Gábor, A. (2016). Neural mechanisms for lexical processing in dogs. *Science*, *353*, 1030–1032. doi:10.1126/science.aaf3777

Andrew, R. J., Mench, J., & Rainey, C. (1982). Right-left asymmetry of response to visual stimuli in the domestic chick. In D. Ingle, M. Goodale, & R. Mansfield (Eds.), *Analysis of visual behaviour* (pp. 197–209). Cambridge, MA: MIT Press.

Anfora, G., Rigosi, E., Frasnelli, E., Ruga, V., Trona, F., & Vallortigara, G. (2011). Lateralization in the invertebrate brain: Left-right asymmetry of olfaction in bumble bee, *Bombus terrestris*. *Plos One*, *6*, e18903. doi:10.1371/journal.pone.0018903

Annett, M. (1985). *Left, right, hand and brain: The right shift theory*. Lawrence Erlbaum Associates London.

Archer, J. (1973). Tests for emotionality in rats and mice: A review. *Animal Behaviour*, *21*, 205–235. doi:10.1016/s0003-3472(73)80065-x

Arnold, M. (1960a). *Emotion and personality. Vol. 1. Psychological aspects.* New York: Columbia University Press.

Arnold, M. (1960b). *Emotion and personality: Vol. 2. Neurological and physiological aspects.* New York: Columbia University Press.

Artelle, K. A., Dumoulin, L. K., & Reimchen, T. E. (2011). Behavioural responses of dogs to asymmetrical tail wagging of a robotic dog replica. *Laterality: Asymmetries of Body, Brain and Cognition*, *16*, 129–135. doi:10.1080/13576500903386700

Austin, N. P., & Rogers, L. J. (2007). Asymmetry of flight and escape turning responses in horses. *Laterality: Asymmetries of Body, Brain and Cognition*, *12*, 464–474. doi:10 . 1080 / 13576500701495307

Austin, N. P., & Rogers, L. J. (2012). Limb preferences and lateralization of aggression, reactivity and vigilance in feral horses, *Equus caballus*. *Animal Behaviour*, *83*, 239–247. doi:10.1016/j.anbehav.2011.10.033

Austin, N. P., & Rogers, L. J. (2014). Lateralization of agonistic and vigilance responses in Przewalski horses (*Equus przewalskii*). *Applied Animal Behaviour Science*, *151*, 43–50. doi:10.1016/j.applanim.2013.11.011

Balconi, M., Grippa, E., & Vanutelli, M. E. (2015). Resting lateralized activity predicts the cortical response and appraisal of emotions: an fNIRS study. *Social Cognitive and Affective Neuroscience*, *10*, 1607–1614. doi:10.1093/scan/nsv041

Balconi, M., & Mazza, G. (2010). Lateralisation effect in comprehension of emotional facial expression: A comparison between EEG alpha band power and behavioural inhibition (BIS) and activation (BAS) systems. *Laterality: Asymmetries of Body, Brain and Cognition*, *15*, 361–384. doi:10.1080/13576500902886056

Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M. J., & Van Ijzendoorn, M. H. (2007). Threat-related attentional bias in anxious and nonanxious individuals: A meta-analytic study. *Psychological Bulletin*, *133*, 1–24. doi:10.1037/0033-2909.133.1.1

Barnard, S., Matthews, L., Messori, S., Podaliri-Vulpiani, M., & Ferri, N. (2015). Laterality as an indicator of emotional stress in ewes and lambs during a separation test. *Animal Cognition*, *19*, 207–214. doi:10.1007/s10071-015-0928-3

Barnard, S., Wells, D. L., & Hepper, P. G. (2018). Laterality as a predictor of coping strategies in dogs entering a rescue shelter. *Symmetry*, *10*, 538. doi:10.3390/sym10110538

Barnard, S., Wells, D. L., Hepper, P. G., & Milligan, A. D. S. (2017). Association between lateral bias and personality traits in the domestic dog (*Canis familiaris*). *Journal of Comparative Psychology*, *131*, 246–256. doi:10.1037/com0000074

Baruzzi, C., Nawroth, C., McElligott, A., & Baciadonna, L. (2018). Motor asymmetry in goats during a stepping task. *Laterality: Asymmetries of Body, Brain and Cognition*, *23*, 599–609. doi:10.1080/1357650X.2017.1417993

Batt, L. S., Batt, M. S., Baguley, J. A., & McGreevy, P. D. (2009). The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, *4*, 216–222. doi:10.1016/j.jveb.2009.02.001

Batt, L. S., Batt, M. S., Baguley, J., & McGreevy, P. D. (2008). Stability of motor lateralisation in maturing dogs. *Laterality: Asymmetries of Body, Brain and Cognition*, *13*, 468–479. doi:10.1080/13576500802201505

Beaton, A. A., Kaack, I. H., & Corr, P. J. (2015). Handedness and behavioural inhibition system/behavioural activation system (BIS/BAS) scores: A replication and extension of Wright, Hardie, and Wilson (2009). *Laterality: Asymmetries of Body, Brain and Cognition*, *20*, 585–603. doi:10.1080/1357650X.2015.1016530

Beaton, A. A., Mutinelli, S., & Corr, P. J. (2017). Fractionating negative and positive affectivity in handedness : Insights from the Reinforcement Sensitivity Theory of personality. *Laterality: Asymmetries of Body, Brain and Cognition*, *22*, 419–444. doi:10.1037/pas000

Bellegarde, L. G., Haskell, M. J., Duvaux-Ponter, C., Weiss, A., Boissy, A., & Erhard, H. W. (2017). Face-based perception of emotions in dairy goats. *Applied Animal Behaviour Science*, *193*, 51–59. doi:10.1016/j.applanim.2017.03.014

Bentham, J. (1781). *An Introduction to the Principles of Morals and Legislation*. McMaster University Archive for the History of Economic Thought.

Berckmans, D. (2017). General introduction to precision livestock farming. *Animal Frontiers*, *7*, 6–11. doi:10.2527/af.2017.0102

Berkman, E. T., & Lieberman, M. D. (2010). Approaching the Bad and avoiding the Good: Lateral prefrontal cortical asymmetry distinguishes between action and valence. *Journal of Cognitive Neuroscience*, *22*, 1970–1979. doi:10.1162/jocn.2009.21317.Approaching

Berkman, E. T., Lieberman, M. D., & Gable, S. L. (2009). BIS, BAS, and response conflict: Testing predictions of the revised Reinforcement Sensitivity Theory. *Personality and Individual Differences*, *46*, 586–591. doi:10.1016/j.paid.2008.12.015.BIS

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*, 361–368. doi:10.1016/j.tree.2008.04.003

Bisazza, A., Cantalupo, C., Capocchiano, M., & Vallortigara, G. (2000). Population lateralisation and social behaviour: A study with 16 species of fish. *Laterality: Asymmetries of Body, Brain and Cognition*, *5*, 269–284. doi:10.1080/713754381

Bisazza, A., Pignatti, & Vallortigara, G. (1997). Laterality in detour behaviour: Interspecific variation in poeciliid fish. *Animal behaviour*, *54*, 1273–81. doi:10.1006/anbe.1997.0522

Bisazza, A., Rogers, L. J., & Vallortigara, G. (1998). The origins of cerebral asymmetry: A review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neuroscience and Biobehavioral Reviews*, *22*, 411–426. doi:10.1016/s0149-7634(97)00050-x

Board, S. (2002). *Ecological Relations: Towards an Inclusive Politics of the Earth* (Routledge). London: Taylor and Francis.

Boissy, A. (2019). How to access animal sentience ? The close relationship between emotions and cognition. In S. Hild & L. Schweitzer (Eds.), *Animal welfare: From science to law* (pp. 21–31).

Boissy, A., Bouix, J., Orgeur, P., Poindron, P., Bibé, B., & Neindre, P. L. (2005). Genetic analysis of emotional reactivity in sheep: Effects of the genotypes of the lambs and of their dams. *Genetics Selection Evolution*, *37*, 381–401. doi:10.1051/gse:2005007

Boissy, A., & Erhard, H. W. (2014). How studying interactions between animal emotions, cognition, and personality can contribute to improve farm animal welfare. In T. Grandin & M. J. Deesing (Eds.), *Genetics and the behavior of domestic animals*. Academic press.

Boissy, A., Manteuffel, G., Jensen, M. B., Moe, R. O., Spruijt, B., Keeling, L. J., Winckler, C., Forkman, B., Dimitrov, I., Langbein, J., Bakken, M., Veissier, I., & Aubert, A. (2007). Assessment of positive emotions in animals to improve their welfare. *Physiology & Behavior*, *92*, 375–397. doi:10.1016/j.physbeh.2007.02.003

Bolhuis, J. E., Schouten, W. G. P., Leeuw, J. A., Schrama, J. W., & Wiegant, V. M. (2004). Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioural Brain Research*, *152*, 351–360. doi:10.1016/j.bbr.2003.10.024

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2005a). Behavioural development of pigs with different coping characteristics in barren and substrate-enriched housing conditions. *Applied Animal Behaviour Science*, *93*, 213–228. doi:10.1016/j.applanim.2005.01.006

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2005b). Individual coping characteristics, aggressiveness and fighting strategies in pigs. *Animal Behaviour*, *69*, 1085–1091. doi:10.1016/j.anbehav.2004.09.013

Bolhuis, J. E., Schouten, W. G. P., Schrama, J. W., & Wiegant, V. M. (2006). Effects of rearing and housing environment on behaviour and performance of pigs with different coping characteristics. *Applied Animal Behaviour Science*, *101*, 68–85. doi:10.1016/j.applanim.2006.01.001

Bosse, M., Megens, H. J., Frantz, L. A. F., Madsen, O., Larson, G., Paudel, Y., Duijvesteijn, N., Harlizius, B., Hagemeijer, Y., Crooijmans, R. P. M. A., & Groenen, M. A. M. (2014). Genomic analysis reveals selection for Asian genes in European pigs following human-mediated introgression. *Nature Communications*, *5*, 1–8. doi:10.1038/ncomms5392

Braccini, S. N., & Caine, N. G. (2009). Hand preference predicts reactions to novel foods and predators in marmosets (*Callithrix geoffroyi*). *Journal of Comparative Psychology*, *123*, 18–25. doi:10.1037/a0013089

Braccini, S. N., Lambeth, S. P., Schapiro, S. J., & Fitch, W. T. (2012). Eye preferences in captive chimpanzees. *Animal Cognition*, *15*, 971–978. doi:10.1007/s10071-012-0523-9

Bracha, H. S., Seitz, D. J., Otemaa, J., & Glick, S. D. (1987). Rotational movement (circling) in normal humans: Sex difference and relationship to hand, foot and eye preference. *Brain Research*, *411*, 231–235. doi:10.1016/0006-8993(87)91074-2

Brambell Committee Report. (1965). *Report of the technical committee to enquire into the welfare of animals kept under intensive livestock husbandry systems*. London: Her Majesty's Stationery Office (HMSO).

Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference strength and noise phobia in *Canis familiaris*. *Journal of Comparative Psychology*, *120*, 176–183. doi:10.1037/0735-7036.120.3.176

Briefer, E. F. (2012). Vocal expression of emotions in mammals: Mechanisms of production and evidence. *Journal of Zoology*, *288*, 1–20. doi:10.1111/j.1469-7998.2012.00920.x

Briefer, E. F., Vizier, E., Gygax, L., & Hillmann, E. (2019a). Expression of emotional valence in pig closed-mouth grunts: Involvement of both source- and filter-related parameters. *The Journal of the Acoustical Society of America*, *145*, 2895–2908. doi:10.1121/1.5100612

Briefer, E. F., Linhart, P., Policht, R., Špinka, M., Leliveld, L. M. C., Düpjan, S., Puppe, B., de la Torre, M. P., Janczak, A. M., Bourguet, C., Deiss, V., Boissy, A., Guérin, C., Read, E., Coulon, M., Hillmann, E., & Tallet, C. (2019b). Vocal expression of emotional valence in pigs across multiple call types and contexts. *PeerJ Preprints*, 7:e27934v1. doi:10.7287/peerj.preprints.27934v1

Broca, P. (1861a). Perte de la parole, ramollissement chronique et destruction partielle du lobe antérieur gauche du cerveau. *Bulletin de la Société Anthropologique*.

Broca, P. (1861b). Remarques sur le siège de la faculté du langage articulé, suivies d'une observation d'aphémie (perte de la parole) [Remarks on the seat of the faculty of articulated lan-

guage, following an observation of aphemia (loss of speech)]. *Bulletin de la Société Anatomique*, *6*, 330–357. doi:10.1111/j.1536-7150.2007.00528.x

Broom, D. M. (1986). Indicators of poor welfare. *British Veterinary Journal*, *142*, 524–526. doi:10.1016/0007-1935(86)90109-0

Broom, D. M. (1991). Animal welfare: Concepts and measurements. *Journal of Animal Science*, *69*, 4167–4175.

Broom, D. M. (2010a). Animal welfare: An aspect of care, sustainability, and food quality required by the public. *Journal of Veterinary Medical Education*, *37*, 83–88. doi:10.3138/jvme.37.1.83

Broom, D. M. (2010b). Cognitive ability and awareness in domestic animals and decisions about obligations to animals. *Applied Animal Behaviour Science*, *126*, 1–11. doi:10.1016/j.applanim.2010.05.001

Broom, D. M. (2011). A history of animal welfare science. *Acta Biotheoretica*, *59*, 121–137. doi:10.1007/s10441-011-9123-3

Broom, D. M. (2016). World impact of ISAE: past and future. In *Animals and us: 50 years and more of applied ethology* (Chap. 14, pp. 269–278). doi:10.3920/978-90-8686-828-5_14

Broom, D. M., Sena, H., & Moynihan, K. L. (2009). Pigs learn what a mirror image represents and use it to obtain information. *Animal Behaviour*, *78*, 1037–1041. doi:10.1016/j.anbehav.2009.07.027

Brosch, T., Scherer, K., Grandjean, D., & Sander, D. (2013). The impact of emotion on perception, attention, memory, and decision-making. *Swiss Medical Weekly*, *143*, w13786. doi:10.4414/smw.2013.13786

Brown, C., & Bibost, A.-L. (2014). Laterality is linked to personality in the black-lined rainbowfish, *Melanotaenia nigrans*. *Behavioral Ecology and Sociobiology*, *68*, 999–1005. doi:10.1007/s00265-014-1712-0

Brown, J. A., Dewey, C., Delange, C. F. M., Mandell, I. B., Purslow, P. P., Robinson, J. A., Squires, E. J., & Widowski, T. M. (2009). Reliability of temperament tests on finishing pigs in group-housing and comparison to social tests. *Applied Animal Behaviour Science*, *118*, 28–35. doi:10.1016/j.applanim.2009.02.005

Buckholtz, J. W., & Meyer-Lindenberg, A. (2008). MAOA and the neurogenetic architecture of human aggression. *Trends in Neurosciences*, *31*, 120–129. doi:10.1016/j.tins.2007.12.006

Buller, H., Blokhuis, H., Jensen, P., & Keeling, L. (2018). Towards farm animal welfare and sustainability. *Animals*, *8*, 1–13. doi:10.3390/ani8060081

Burgdorf, J., & Panksepp, J. (2006). The neurobiology of positive emotions. *Neuroscience and Biobehavioral Reviews*, *30*, 173–187. doi:10.1016/j.neubiorev.2005.06.001

Burghardt, G. M. (2018). Anthropomorphism. *Encyclopedia of Animal Cognition and Behavior*, 1–4. doi:10.1007/978-3-319-47829-6

Burghardt, G. M. (2019). A place for emotions in behavior systems research. *Behavioural Processes*, *166*, 103881. doi:10.1016/j.beproc.2019.06.004

Burne, T. H., Murfitt, P. J., & Gilbert, C. L. (2000). Deprivation of straw bedding alters PGF(2α)-induced nesting behaviour in female pigs. *Applied Animal Behaviour Science*, *69*, 215–225. doi:10.1016/S0168-1591(00)00135-0

Bushby, E. V., Friel, M., Goold, C., Gray, H., Smith, L., & Collins, L. M. (2018). Factors influencing individual variation in farm animal cognition and how to account for these statistically. *Frontiers in Veterinary Science*, *5*, 1–15. doi:10.3389/fvets.2018.00193

Byrnes, E. E., Pouca, C. V., Chambers, S. L., & Brown, C. (2016a). Into the wild: Developing field tests to examine the link between elasmobranch personality and laterality. *Behaviour*, *153*, 1777–1793. doi:10.1163/1568539X-00003373

Byrnes, E. E., Vila-Pouca, C., & Brown, C. (2016b). Laterality strength is linked to stress reactivity in Port Jackson sharks (*Heterodontus portusjacksoni*). *Behavioural Brain Research*, *305*, 239–246. doi:10.1016/j.bbr.2016.02.033

Cabanac, M. (1992). Pleasure: The common currency. *Journal of Theoretical Biology*, *155*, 173–200. doi:10.1016/S0022-5193(05)80594-6

Cabanac, M. (2002). What is emotion? *Behavioural Processes*, *60*, 69–83. doi:10 . 1016 / s0376 - 6357(02)00078-5

Cafazzo, S., & Natoli, E. (2009). The social function of tail up in the domestic cat (*Felis silvestris catus*). *Behavioural Processes*, *80*, 60–66. doi:10.1016/j.beproc.2008.09.008

Cai, Q., der Haegen, L. V., & Brysbaert, M. (2013). Complementary hemispheric specialization for language production and visuospatial attention. *Proceedings of the National Academy of Sciences*, *110*, E322–E330. doi:10.1073/pnas.1212956110

Camerlink, I. (2019). New perspectives for assessing the valence of social interactions. In R. C. Newberry & B. O. Braastad (Eds.), *53rd congress of the ISAE, animal lives worth living* (p. 250). Bergen: Wageningen Academic Publishers.

Camerlink, I., Menneson, S., Turner, S. P., Farish, M., & Arnott, G. (2018a). Lateralization influences contest behaviour in domestic pigs. *Scientific Reports*, *8*, 12116. doi:10.1038/s41598-018-30634-z

Camerlink, I., Coulange, E., Farish, M., Baxter, E. M., & Turner, S. P. (2018b). Facial expression as a potential measure of both intent and emotion. *Scientific Reports*, *8*, 1–9. doi:10.1038/s41598-018-35905-3

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*): Problem solving and responses in a novel setting. *Journal of Comparative Psychology*, *113*, 149–157. doi:10.1037/0735-7036.113.2.149

Cancela, L., Basso, A., Martijena, I., Capriles, N., & Molina, V. (2001). A dopaminergic mechanism is involved in the 'anxiogenic-like'response induced by chronic amphetamine treatment: A behavioral and neurochemical study. *Brain research*, *909*, 179–186. doi:10.1016/S0006-8993(01)02680-4

Cannon, W. B. (1929). *Bodily changes in pain, hunger, fear and rage: An account of recent researches into the function of emotional excitement.* (2nd Edition). New York: Appleton-Century Co.

Cardoso, G. C. (2013). Using frequency ratios to study vocal communication. *Animal Behaviour*, *85*, 1529–1532. doi:10.1016/j.anbehav.2013.03.044

Careau, V., Thomas, D. K., Humphries, M. M., & Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, *117*, 641–653. doi:10.1111/j.2008.0030-1299.16513.x

Carere, C., Caramaschi, D., & Fawcett, T. (2010). Covariation between personalities and individual differences in coping with stress: Converging evidence and hypotheses. *Current Zoology*, *56*, 728–740.

Carnevali, L., Koenig, J., Sgoifo, A., & Ottaviani, C. (2018). Autonomic and brain morphological predictors of stress resilience. *Frontiers in Neuroscience*, *12*, 1–13. doi:10.3389/fnins.2018.00228

Carone, G. R. (2005). Mind and body in late Plato. *Archiv fur Geschichte der Philosophie*, *87*, 227–269. doi:10.1515/agph.2005.87.3.227

Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlishaw, G., & Heinsohn, R. (2013). Animal personality: What are behavioural ecologists measuring? *Biological Reviews*, *88*, 465–475. doi:10.1111/brv.12007

Carver, C. S., & Harmon-Jones, E. (2009). Anger is an approach-related affect : Evidence and implications. *Psychological Bulletin*, *135*, 183–204. doi:10.1037/a0013965

Chance, S. A., & Crow, T. J. (2007). Distinctively human: Cerebral lateralisation and language in *Homo sapiens*. *Journal of Anthropological Sciences*, *85*, 83–100. doi:10 . 1080 / 00397910701577570

Chester, D. S., Dewall, C. N., Derefinko, K. J., Estus, S., Jessica, R., Lynam, D. R., & Jiang, Y. (2015). Monoamine oxidase A (MAOA) genotype predicts greater aggression through impulsive reactivity to negative affect. *Behavioural Brain Research*, *283*, 97–101. doi:10.1016/j.bbr.2015.01.034.

Chivers, D. P., McCormick, M. I., Warren, D. T., Allan, B. J., Ramasamy, R. A., Arvizu, B. K., Glue, M., & Ferrari, M. C. (2017). Competitive superiority versus predation savvy: The two sides of behavioural lateralization. *Animal Behaviour*, *130*, 9–15. doi:10.1016/j.anbehav.2017.05.006

Chivers, D. P., Mccormick, M. I., Allan, B. J. M., Bryshun, R., Ferrari, M. C. O., Mitchell, D., Gonc, E. J., Bjm, A., & Chivers, D. P. (2016). At odds with the group : Changes in lateralization and escape performance reveal conformity and conflict in fish schools. *Proceedings of the Royal Society B*, 1–8. doi:10.1098/rspb.2016.1127

Chou, J.-Y., O'Driscoll, K., D'Eath, R. B., Sandercock, D. A., & Camerlink, I. (2019). Multi-step tail biting outbreak intervention protocols for pigs housed on slatted floors. *Animals*, *9*, 582. doi:10.3390/ani9080582

Clara, E., Tommasi, L., & Rogers, L. J. (2008). Social mobbing calls in common marmosets (*Callithrix jacchus*): Effects of experience and associated cortisol levels. *Animal Cognition*, *11*, 349–358. doi:10.1007/s10071-007-0125-0

Coan, J. A., & Allen, J. J. B. (2003). Frontal EEG asymmetry and the behavioral activation and inhibition systems. *Psychophysiology*, *40*, 106–114. doi:10.1111/1469-8986.00011

Colditz, I. G., & Hine, B. C. (2016). Resilience in farm animals: Biology, management, breeding and implications for animal welfare. *Animal Production Science*, *56*, 1961–1983. doi:10.1071/AN15297

Collins, R. L. (1975). When left-handed mice live in right-handed worlds. *Science*, *187*, 181–184. doi:10.1126/science.1111097

Corballis, M. C. (2009). The evolution and genetics of cerebral asymmetry. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 867–879. doi:10.1098/rstb.2008.0232

Cornwell, J. F. M., Franks, B., & Higgins, E. T. (2014). Truth , control , and value motivations : The " what ," " how ," and " why " of approach and avoidance. *Frontiers in Systems Neuroscience*, *8*, 1–15. doi:10.3389/fnsys.2014.00194

Corr, P. J. (2009). The Reinforcement Sensitivity Theory of personality. In P. J. Corr & G. Matthews (Eds.), *The Cambridge handbook of personality psychology* (Chap. 21, pp. 347–376). Cambridge University Press.

Cox, E., Ruge, L., Mancini, C., & Luck, R. (2018). User centered design approaches to measuring canine behavior: tail wagging as a measure of user experience. In *Aci2018 proceedings of the fifth international conference on animal-computer interaction* (pp. 1–12). doi:10.1145/3295598.3295599

Craig, a. D. B. (2005). Forebrain emotional asymmetry: A neuroanatomical basis? *Trends in Cognitive Sciences*, *9*, 566–71. doi:10.1016/j.tics.2005.10.005

Crump, A., Arnott, G., & Bethell, E. (2018). Affect-driven attention biases as animal welfare indicators: Review and methods. *Animals*, *8*, 136. doi:10.3390/ani8080136

D'Eath, R. B., & Turner, S. P. (2009). The natural behaviour of the pig. In J. N. Marchant-Forde (Ed.), *The welfare of pigs* (pp. 13–45). Dordrecht: Springer Netherlands.

D'Ingeo, S., Quaranta, A., Siniscalchi, M., Stomp, M., Coste, C., Bagnard, C., Hausberger, M., & Cousillas, H. (2019). Horses associate individual human voices with the valence of past interactions: A behavioural and electrophysiological study. *Scientific Reports*, *9*, 11568. doi:10.1038/s41598-019-47960-5

Dadda, M., Zandonà, E., & Bisazza, A. (2007). Emotional responsiveness in fish from lines artificially selected for a high or low degree of laterality. *Physiology & Behavior*, *92*, 764–772. doi:10.1016/j.physbeh.2007.06.001

Dalgleish, T. (2004). The Emotional Brain. *Nature Reviews Neuroscience*, *5*, 282–289. doi:10.2307/3953278

Damasio, A. R. (1994). *Descartes' error: emotion, reason and the human brain*. New York: G.P. Putnam's Sons.

Damasio, A. R. (1995). Toward a neurobiology of emotion and feeling: Operational concepts and hypotheses. *The Neuroscientist*, *1*, 19–25. doi:10.1177/107385849500100104

Darwin, C. (1859). *On the origin of the species*. John Murray.

Darwin, C. (1873). *The expression of the emotions in man and animals*. John Murray.

Davidson, R. J. (1984). Affect, cognition and hemispheric specialization. In C. E. Izard, J. Kagan, & R. B. Zajonc (Eds.), *Emotions, cognition, and behavior* (Chap. 11, pp. 320–365). New York: Cambridge University Press.

Davidson, R. J. (1992a). Anterior cerebral asymmetry and the nature of emotion. *Brain and Cognition*, *20*, 125–151. doi:10.1016/0278-2626(92)90065-T

Davidson, R. J. (1992b). Emotion and affective style - Hemispheric substrates. *Psychological Science*, *3*, 39–43. doi:10.1111/j.1467-9280.1992.tb00254.x

Davidson, R. J. (1998). Affective style and affective disorders: Perspectives from affective neuroscience. *Cognition & Emotion*, *12*, 307–330. doi:10.1080/026999398379628

Davidson, R. J. (2001). Toward a biology of personality and emotion. *Annals of the New York Academy of Sciences*, *935*, 191–207. doi:10.1111/j.1749-6632.2001.tb03481.x

Davidson, R. J. (2004). Well-being and affective style: Neural substrates and biobehavioural correlates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*, 1395–1411. doi:10.1098/rstb.2004.1510

Davidson, R. J., & Fox, N. A. (1989). Frontal brain asymmetry predicts infants' response to maternal separation. *Journal of Abnormal Psychology*, *98*, 127–131. doi:10.1037/0021-843X.98.2.127

Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences*, *3*, 11–21. doi:10.1016/S1364-6613(98)01265-0

Davidson, R. J., Schwartz, G. E., Saron, E., Bennett, J., & Goleman, D. (1979). Frontal versus parietal EEG asymmetry during positive and negative affect. *Psychophysiology*, *16*, 202–203.

Dawkins, M. S. (1980). *Animal suffering – The science of animal welfare*. Springer Netherlands.

Dawkins, M. S. (1990). From an animal's point of view: Motivation, fitness, and animal welfare. *Behavioral and Brain Sciences*, *13*, 1–61. doi:10.1017/s0140525x00077104

Dawkins, M. S. (2015). Animal welfare and the paradox of animal consciousness. In *Advances in the study of behavior* (Vol. 47, pp. 5–38). Elsevier Ltd.

De Boyer Des Roches, A., Richardyris, M., Henry, S., Ezzaouia, M., & Hausberger, M. (2008). Laterality and emotions: Visual laterality in the domestic horse (*Equus caballus*) differs with objects' emotional value. *Physiology & Behavior*, *94*, 487–490. doi:10.1016/j.physbeh.2008.03.002

De Latude, M., Demange, M., Bec, P., & Blois-Heulin, C. (2009). Visual laterality responses to different emotive stimuli by red-capped mangabeys, *Cercocebus torquatus torquatus*. *Animal Cognition*, *12*, 31–42. doi:10.1007/s10071-008-0166-z

De Pascalis, V., Cozzuto, G., Caprara, G. V., & Alessandri, G. (2013). Relations among EEG-alpha asymmetry, BIS/BAS, and dispositional optimism. *Biological Psychology*, *94*, 198–209. doi:10.1016/j.biopsycho.2013.05.016

de Waal, F. B. (1999). Anthropomorphism and anthropodenial: Consistency in our thinking about humans and other animals. *Philosophical Topics*, *27*, 255–280. doi:10.1177/109442810034002

DeCatanzaro, D. A. (1999). *Motivation and emotion: Evolutionary, physiological, developmental, and social perspectives*. Prentice-Hall, Inc.

DeGrazia, D. (1996). *Taking animals seriously : mental life and moral status*. Cambridge University Press.

Delgado, M. M., & Sulloway, F. J. (2017). Attributes of conscientiousness throughout the animal kingdom: An empirical and evolutionary overview. *Psychological Bulletin*, *143*, 823–867. doi:10.1037/bul0000107

Demaree, H. A., Everhart, D. E., Youngstrom, E. A., & Harrison, D. W. (2005). Brain lateralization of emotional processing: historical roots and a future incorporating "dominance". *Behavioral and cognitive neuroscience reviews*, *4*, 3–20. doi:10.1177/1534582305276837

Denenberg, V. H., Rosen, G. D., Hofmann, M., Gall, J., Stockler, J., & Yutzey, D. A. (1982). Neonatal postural asymmetry and sex differences in the rat. *Developmental Brain Research*, *2*, 417–419. doi:10.1016/0165-3806(81)90048-1

Depue, R. A., & Collins, P. F. (1999). Neurobiology of the structure of personality: Dopamine, facilitation of incentive motivation, and extraversion. *Behavioral and Brain Sciences*, *22*, 491–517.

Descartes, R. (1637). *Discours de la méthode*.

Descovich, K. A., Wathan, J., Leach, M. C., Buchanan-Smith, H. M., Flecknell, P., Farningham, D., & Vick, S. J. (2017). Facial expression: An under-utilized tool for the assessment of welfare in mammals. *Altex*, *34*, 409–429. doi:10.14573/altex.1607161

Désiré, L., Boissy, A., & Veissier, I. (2002). Emotions in farm animals: A new approach to animal welfare in applied ethology. *Behavioural Processes*, *60*, 165–180. doi:10.1016/S0376-6357(02)00081-5

Désiré, L., Veissier, I., Després, G., & Boissy, A. (2004). On the way to assess emotions in animals: do lambs (*Ovis aries*) evaluate an event through its suddenness, novelty, or unpredictability? *Journal of Comparative Psychology*, *118*, 363–374. doi:10.1037/0735-7036.118.4.363

DeYoung, C. G. (2013). The neuromodulator of exploration : A unifying theory of the role of dopamine in personality. *Frontiers in Human Neuroscience*, *7*, 1–26. doi:10.3389/fnhum.2013.00762

DeYoung, C. G., Hirsh, J. B., Shane, M. S., Papademetris, X., Rajeevan, N., & Gray, J. R. (2010). Testing predictions from personality neuroscience: Brain structure and the big five. *Psychological Science*, *21*, 820–828. doi:10.1177/0956797610370159.Testing

Dingemanse, N. J., & Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*, 3947–3958. doi:10.1098/rstb.2010.0221

Dippel, S., & Schrader, L. (2016). Tail docking in pigs - status quo in Germany. *Züchtungskunde*, *88*, 417–428.

Domenici, P., Allan, B., McCormick, M. I., & Munday, P. L. (2011). Elevated carbon dioxide affects behavioural lateralization in a coral reef fish. *Biology Letters*, *8*, 78–81. doi:10.1098/rsbl.2011.0591

Donald, R. D., Healy, S. D., Lawrence, A. B., & Rutherford, K. M. D. (2011). Emotionality in growing pigs: Is the open field a valid test? *Physiology & Behavior*, *104*, 906–913. doi:10.1016/j.physbeh.2011.05.031

Done, S. (2011). Tail biting: thoughts on causation with particular reference to anatomy and the porcine brain. *Pig Journal*, *66*, 103–117.

Douglas, C., Bateson, M., Walsh, C., Bédué, A., & Edwards, S. A. (2012). Environmental enrichment induces optimistic cognitive biases in pigs. *Applied Animal Behaviour Science*, *139*, 65–73. doi:10.1016/j.applanim.2012.02.018

Duncan, I. J. H. (1993). Welfare is to do with what animals feel. *Journal of Agricultural and Environmental Ethics*, *6*, 8–14.

Duncan, I. J. H. (2006). The changing concept of animal sentience. *Applied Animal Behaviour Science*, *100*, 11–19. doi:10.1016/j.applanim.2006.04.011

Duncan, I. J. H. (2020). The philosophical and biological evolution of feelings in well-being. In F. D. McMillan (Ed.), *Mental health and well-being in animals* (2nd, Chap. 3, pp. 21–32). CABI.

Duncan, I. J. H., & Dawkins, M. S. (1983). The Problem of Assessing "Well-Being" and "Suffering" in Farm Animals. *Indicators Relevant to Farm Animal Welfare*, 13–24. doi:10.1007/978-94-009-6738-0_2

Düpjan, S., Stracke, J., Tuchscherer, A., & Puppe, B. (2017). An improved design for the spatial judgement task in domestic pigs. *Applied Animal Behaviour Science*, *187*, 23–30. doi:10.1016/j.applanim.2016.11.012

Düpjan, S., Tuchscherer, A., Langbein, J., Schön, P.-C., Manteuffel, G., & Puppe, B. (2011). Behavioural and cardiac responses towards conspecific distress calls in domestic pigs (*Sus scrofa*). *Physiology & Behavior*, *103*, 445–452. doi:10.1016/j.physbeh.2011.03.017

Eklund, B., & Jensen, P. (2011). Domestication effects on behavioural synchronization and individual distances in chickens (*Gallus gallus*). *Behavioural Processes*, *86*, 250–256. doi:10.1016/j.beproc.2010.12.010

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science*, *306*, 1903–1907. doi:10.1126/science.1098410

Erdle, S., & Rushton, J. P. (2010). The General Factor of Personality, BIS-BAS, expectancies of reward and punishment, self-esteem, and positive and negative affect. *Personality and Individual Differences*, *48*, 762–766. doi:10.1016/j.paid.2010.01.025

Esch, L., Wöhr, C., Erhard, M., & Krüger, K. (2019). Horses' (*Equus caballus*) laterality, stress hormones, and task related behavior in innovative problem-solving. *Animals*, *9*, 265. doi:10.3390/ani9050265

Espmark, Y., & Kinderås, K. (2002). Behavioural lateralisation in reindeer. *Rangifer*, *22*, 51. doi:10.7557/2.22.1.687

Fagot, J., & Vauclair, J. (1991). Manual laterality in nonhuman primates: A distinction between handedness and manual specialization. *Psychological Bulletin*, *109*, 76–89. doi:10.1037//0033-2909.109.1.76

Fahim, A. D., Kamboj, M. L., Bhakat, M., Mohanty, T. K., & Gupta, R. (2018). Preference of side and standing in relationship with milking characteristics and temperament score of crossbred dairy cows in an 8 × 2 herringbone milking parlour. *Turkish Journal of Veterinary and Animal Sciences*, *42*, 49–54. doi:10.3906/vet-1705-1

Fang, M., Li, J., Rudd, J. A., Wai, S. M., Yew, J. C., & Yew, D. T. (2006). fMRI Mapping of cortical centers following visual stimulation in postnatal pigs of different ages. *Life Sciences*, *78*, 1197–1201. doi:10.1016/j.lfs.2005.06.030

FAO Stats. (2017). Food and agriculture organization of the united nations, Rome.

Farmer, K., Krueger, K., & Byrne, R. W. (2010). Visual laterality in the domestic horse (*Equus caballus*) interacting with humans. *Animal Cognition*, *13*, 229–238. doi:10.1007/s10071-009-0260-x

Feddes, J. J. R., & Fraser, D. (1994). Non-nutritive chewing by pigs: Implications for tail-biting and behavioral enrichment. *Transactions of the ASAE*, *37*, 947–950. doi:10.13031/2013.28163

Fernández-Lázaro, G., Latorre, R., Alonso-García, E., & Barja Núñez, I. (2019). Nonhuman primate welfare: Can there be a relationship between personality, lateralization and physiological indicators? *Behavioural Processes*, *166*, 103897. doi:10.1016/j.beproc.2019.103897

Ferrari, M. C., McCormick, M. I., Mitchell, M. D., Allan, B. J., Gonçalves, E. J., & Chivers, D. P. (2017). Daily variation in behavioural lateralization is linked to predation stress in a coral reef fish. *Animal Behaviour*, *133*, 189–193. doi:10.1016/j.anbehav.2017.09.020

Fidler, A. E., van Oers, K., Drent, P. J., Kuhn, S., Mueller, J. C., & Kempenaers, B. (2007). Drd4 gene polymorphisms are associated with personality variation in a passerine bird. *Proceedings of the Royal Society B*, *274*, 1685–1691. doi:10.1098/rspb.2007.0337

Finkemeier, M.-A., Langbein, J., & Puppe, B. (2018). Personality research in mammalian farm animals: Concepts, measures, and relationship to welfare. *Frontiers in Veterinary Science*, *5*, 131. doi:10.3389/fvets.2018.00131

Foris, B., Zebunke, M., Langbein, J., & Melzer, N. (2019). Comprehensive analysis of affiliative and agonistic social networks in lactating dairy cattle groups. *Applied Animal Behaviour Science*, *210*, 60–67. doi:10.1016/j.applanim.2018.10.016

Forkman, B., Boissy, A., Meunier-Salaün, M.-C., Canali, E., & Jones, R. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology & Behavior*, *92*, 340–374. doi:10.1016/j.physbeh.2007.03.016

Forkman, B., Furuhaug, I. L., & Jensen, P. (1995). Personality, coping patterns, and aggression in piglets. *Applied Animal Behaviour Science*, *45*, 31–42. doi:10.1016/0168-1591(95)00601-N

Forrester, G. S. (2017). Hand, limb, and other motor preferences. In L. J. Rogers & G. Vallortigara (Eds.), *Lateralized Brain Functions: Methods in Human and Non-Human Species* (pp. 121–152). New York: Springer New York.

Found, R., & St. Clair, C. C. (2017). Ambidextrous ungulates have more flexible behaviour, bolder personalities and migrate less. *Royal Society Open Science*, *4*, 160958. doi:10 . 1098 / rsos . 160958

Foury, A., Geverink, N. A., Gil, M., Gispert, M., Hortós, M., Font I Furnols, M., Carrion, D., Blott, S. C., Plastow, G. S., & Mormède, P. (2007). Stress neuroendocrine profiles in five pig breeding lines and the relationship with carcass composition. *Animal*, *1*, 973–982. doi:10.1017/S1751731107000249

Franks, B. (2019). What do animals want? *Animal Welfare*, *28*, 1–10. doi:10.7120/09627286.28.1.001

Franks, B., Higgins, E. T., & Champagne, F. A. (2012). Evidence for individual differences in regulatory focus in rats , *Rattus norvegicus*. *Journal of Comparative Psychology*, *126*, 347–354. doi:10.1037/a0027244

Franks, B., Higgins, E. T., & Champagne, F. A. (2014). A theoretically based model of rat personality with implications for welfare. *Plos One*, *9*, e95135. doi:10.1371/journal.pone.0095135

Franks, B., Reiss, D., Cole, P., Friedrich, V., Thompson, N., & Higgins, E. T. (2013). Predicting how individuals approach enrichment : Regulatory focus in cotton-top tamarins (*Sanguinus oedipus*). *Zoo Biology*, *435*, 427–435. doi:10.1002/zoo.21075

Frantz, L. A. F., Schraiber, J. G., Madsen, O., Megens, H. J., Cagan, A., Bosse, M., Paudel, Y., Crooijmans, R. P. . A., Larson, G., & Groenen, M. A. M. (2015). Evidence of long-term gene flow and selection during domestication from analyses of Eurasian wild and domestic pig genomes. *Nature Genetics*, *47*, 1141–1148. doi:10.1038/ng.3394

Fraser, D. (2008). *Understanding animal welfare*. Acta Veterinaria Scandinavica.

Frasnelli, E. (2013). Brain and behavioral lateralization in invertebrates. *Frontiers in Psychology*, *4*, 939. doi:10.3389/fpsyg.2013.00939

Frasnelli, E., & Vallortigara, G. (2018). Individual-level and population-level lateralization: Two sides of the same coin. *Symmetry*, *10*, 739. doi:10.3390/sym10120739

Freud, S. (1904). *Zur Psychopathologie des Alltagslebens (Über Vergessen, Versprechen, Vergreifen, Aberglaube und Irrtum)* (Karger). Berlin.

Freund, J., Brandmaier, A. M., Lewejohann, L., Kirste, I., Kritzler, M., Krüger, A., Sachser, N., Lindenberger, U., & Kempermann, G. (2015). Association between exploratory activity and social individuality in genetically identical mice living in the same enriched environment. *Neuroscience*, *309*, 140–152. doi:10.1016/j.neuroscience.2015.05.027

Freund, J., Brandmaier, A. M., Lewejohann, L., Kirste, I., Kritzler, M., Krüger, A., Sachser, N., Lindenberger, U., & Kempermann, G. (2013). Emergence of individuality in genetically identical mice. *Science*, *340*, 756–760. doi:10.1126/science.1235294

Friel, M., Kunc, H. P., Griffin, K., Asher, L., & Collins, L. M. (2016). Acoustic signalling reflects personality in a social mammal. *Royal Society Open Science*, *3*, 160178. doi:10.1098/rsos.160178

Friel, M., Kunc, H. P., Griffin, K., Asher, L., & Collins, L. M. (2019). Positive and negative contexts predict duration of pig vocalisations. *Scientific Reports*, *9*, 1–7. doi:10.1038/s41598-019-38514-w

Gable, P. A., Neal, L. B., & Threadgill, A. H. (2018). Regulatory behavior and frontal activity: Considering the role of revised-BIS in relative right frontal asymmetry. *Psychophysiology*, *55*, 1–18. doi:10.1111/psyp.12910

Gainotti, G. (2012). Unconscious processing of emotions and the right hemisphere. *Neuropsychologia*, *50*, 205–218. doi:10.1016/j.neuropsychologia.2011.12.005

Gainotti, G. (2018). Emotions and the right hemisphere: Can new data clarify old models? *The Neuroscientist*, *25*, 258–270. doi:10.1177/1073858418785342

Gatto, E., Agrillo, C., Brown, C., & Dadda, M. (2019). Individual differences in numerical skills are influenced by brain lateralization in guppies (*Poecilia reticulata*). *Intelligence*, *74*, 12–17. doi:10.1016/j.intell.2019.04.004

Gendron, M., & Barrett, L. F. (2009). Reconstructing the past: A century of ideas about emotion in psychology. *Emotion Review*, *1*, 316–339. doi:10.1038/jid.2014.371. eprint: NIHMS150003

Ghirlanda, S., Frasnelli, E., & Vallortigara, G. (2009). Intraspecific competition and coordination in the evolution of lateralization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 861–866. doi:10.1098/rstb.2008.0227

Ghirlanda, S., & Vallortigara, G. (2004). The evolution of brain lateralization: A game-theoretical analysis of population structure. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 853–857. doi:10.1098/rspb.2003.2669

Gibbons, J. M. (2009). *Effect of selecting for "Robustness" on temperament in dairy cows* (Doctoral dissertation).

Gieling, E. T., Nordquist, R. E., & van der Staay, F. J. (2011). Assessing learning and memory in pigs. *Animal Cognition*, *14*, 151–173. doi:10.1007/s10071-010-0364-3

Gill, J. C., & Thomson, W. (1956). Observations on the behaviour of suckling pigs. *The British Journal of Animal Behaviour*, *4*, 46–51. doi:10.1016/S0950-5601(56)80022-1

Gizewski, E. R., Schanze, T., Bolle, I., de Greiff, A., Forsting, M., & Laube, T. (2007). Visualization of the visual cortex in minipigs using fMRI. *Research in Veterinary Science*, *82*, 281–286. doi:10.1016/j.rvsc.2006.08.004

Glick, S. D., & Ross, D. A. (1981). Right-sided population bias and lateralization of activity in normal rats. *205*, 222–225.

Gold, J. (1985). Cartesian dualism and the current crisis in medicine — a plea for a philosophical approach: Discussion paper. *Journal of the Royal Society of Medicine*, *78*, 663–666. doi:10.1177/014107688507800813

Goma, A. A., Gareth, P. P., Jashim, U., Eloise, R., Harriet, D., & Phillips, C. J. C. (2018). A forced lateralisation test for dairy cows and its relation to their behaviour. *Applied Animal Behaviour Science*, *207*, 8–19. doi:10.1016/j.applanim.2018.06.008

Gordon, D. J., & Rogers, L. J. (2010). Differences in social and vocal behavior between left- and right-handed common marmosets (*Callithrix jacchus*). *Journal of Comparative Psychology*, *124*, 402–411. doi:10.1037/a0019736

Gordon, D. J., & Rogers, L. J. (2015). Cognitive bias, hand preference and welfare of common marmosets. *Behavioural Brain Research*, *287*, 100–108. doi:10.1016/j.bbr.2015.03.037

Gosling, S. D. (2001). From mice to men: What can we learn about personality from animal research? *Psychological Bulletin*, *127*, 45–86. doi:10.1037//0033-2909.127.1.45

Gosling, S. D., & John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, *8*, 69–75. doi:10.1111/1467-8721.00017

Goursot, C., Düpjan, S., Kanitz, E., Tuchscherer, A., Puppe, B., & Leliveld, L. M. C. (2019). Assessing animal individuality: Links between personality and laterality in pigs. *Current Zoology*, *65*, 541–551. doi:10.1093/cz/zoy071

Goursot, C., Düpjan, S., Tuchscherer, A., Puppe, B., & Leliveld, L. M. C. (2018). Behavioural lateralization in domestic pigs (*Sus scrofa*) – variations between motor functions and individuals. *Laterality: Asymmetries of Body, Brain and Cognition*, *23*, 576–598. doi:10.1080/1357650X.2017.1410555

Grabowska, A., Gut, M., Binder, M., Forsberg, L., & Rymarczyk, K. (2012). Switching handedness : fMRI study of hand motor control in right-handers , left-handers and converted left-handers. *Acta Neurobiologiae Experimentalis*, *72*, 439–451.

Graham, F. K., & Clifton, R. K. (1966). Heart-rate change as a component of the orienting response. *Psychological Bulletin*, *65*, 305–320. doi:10.1037/h0023258

Granero, R., Fernández-Aranda, F., Baño, M., Steward, T., Mestre-Bach, G., Del Pino-Gutiérrez, A., Moragas, L., Mallorquí-Bagué, N., Aymamí, N., Goméz-Peña, M., Tárrega, S., Menchón, J. M., & Jiménez-Murcia, S. (2016). Compulsive buying disorder clustering based on sex, age, onset and personality traits. *Comprehensive Psychiatry*, *68*, 1–10. doi:10.1016/j.comppsych.2016.03.003

Gray, J. A. (1970). The psychophysiological basis of introversion-extraversion. *Behaviour Research and Therapy*, *8*, 249–266. doi:10.1016/0005-7967(70)90069-0

Gray, J. A. (1973). Causal theories of personality and how to test them. In J. R. Royce (Ed.), *Multivariate analysis and psychological theory.* Academic Press.

Gray, J. A. (1991). The neuropsychology of temperament. In J. Strelau & A. Angleitner (Eds.), *Explorations in temperament: International perspectives on theory and measurement* (pp. 105–128). Boston, MA: Springer US.

Gray, J. A., & McNaughton, N. (2000). *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system* (Second Edition). Oxford University Press.

Grey, W. (1993). Anthropocentrism and deep ecology. *Australasian Journal of Philosophy*, *71*, 463–475.

Griffin, D. (1976). *The question of animal awareness: Evolutionary continuity of mental experience*. New York: Rockefeller University Press.

Grimshaw, G. M., & Wilson, M. S. (2013). A sinister plot? Facts, beliefs, and stereotypes about the left-handed personality. *Laterality: Asymmetries of Body, Brain and Cognition*, *18*, 135–151. doi:10.1080/1357650x.2011.631546

Gundlach, H. (1968). Brutfürsorge, Brutpflege, Verhaltensontogenese und Tagesperiodik beim Europäischen Wildschwein. *Ethology*, *25*, 955–995. doi:10.1111/J.1439-0310.1968.TB00054.X

Güntürkün, O. (2003). Adult persistence of head-turning asymmetry. *Nature*, *421*, 711–711. doi:10.1038/421711a

Güntürkün, O. (2012). The convergent evolution of neural substrates for cognition. *Psychological Research*, *76*, 212–219. doi:10.1007/s00426-011-0377-9

Güntürkün, O., & Ocklenburg, S. (2017). Ontogenesis of lateralization. *Neuron*, *94*, 249–263. doi:10.1016/j.neuron.2017.02.045

Gupta, R., Raymond, J. E., & Vuilleumier, P. (2019). Priming by motivationally salient distractors produces hemispheric asymmetries in visual processing. *Psychological Research*, *83*, 1798–1807. doi:10.1007/s00426-018-1028-1

Gygax, L. (2017). Wanting, liking and welfare: The role of affective states in proximate control of behaviour in vertebrates. *Ethology*, *123*, 689–704. doi:10.1111/eth.12655

Gygax, L., Reefmann, N., Wolf, M., & Langbein, J. (2013). Prefrontal cortex activity, sympatho-vagal reaction and behaviour distinguish between situations of feed reward and frustration in dwarf goats. *Behavioural Brain Research*, *239*, 104–114. doi:10.1016/j.bbr.2012.10.052

Gygax, L., & Vögeli, S. (2016). Reactions of sheep towards three sets of emotional stimuli: (In)Consistency in respect to stimulus valence and sheep identity. *Applied Animal Behaviour Science*, *174*, 51–57. doi:10.1016/j.applanim.2015.11.015

Hagemann, D., Waldstein, S. R., & Thayer, J. F. (2003). Central and autonomic nervous system integration in emotion. *Brain and Cognition*, *52*, 79–87. doi:10.1016/S0278-2626(03)00011-3

Hardie, S. M., & Wright, L. (2014). Differences between left- and right-handers in approach/avoidance motivation: Influence of consistency of handedness measures. *Frontiers in Psychology*, *5*, 134. doi:10.3389/fpsyg.2014.00134

Harding, E. J., Paul, E. S., & Mendl, M. (2004). Cognitive bias and affective state. *Nature*, *427*, 312. doi:10.1038/427312a

Harman, W., & Ray, W. J. (1977). Hemispheric activity during affective verbal stimuli: An EEG study. *Neuropsychologia*, *15*, 457–460.

Harmon-Jones, E. (2004). Contributions from research on anger and cognitive dissonance to understanding the motivational functions of asymmetrical frontal brain activity. *Biological Psychology*, *67*, 51–76. doi:10.1016/j.biopsycho.2004.03.003

Harmon-Jones, E., & Allen, J. J. B. (1997). Behavioral activation sensitivity and resting frontal EEG asymmetry: Covariation of putative indicators related to risk for mood disorders. *Journal of Abnormal Psychology*, *106*, 159–163. doi:10.1037//0021-843x.106.1.159

Harmon-Jones, E., & Allen, J. J. B. (1998). Anger and frontal brain activity: EEG asymmetry consistent with approach motivation despite negative affective valence. *Journal of Personality and Social Psychology*, *74*, 1310–6. doi:10.1037/0022-3514.74.5.1310

Harmon-Jones, E., & Gable, P. A. (2018). On the role of asymmetric frontal cortical activity in approach and withdrawal motivation: An updated review of the evidence. *Psychophysiology*, *55*, e12879. doi:10.1111/psyp.12879

Harmon-Jones, E., Harmon-Jones, C., & Price, T. F. (2013). What is approach motivation? *Emotion Review*, *5*, 291–295. doi:10.1177/1754073913477509

Harris, L. J. (2019). The discovery of cerebral specialization. *Frontiers of Neurology and Neuroscience*, *44*, 1–14. doi:10.1159/000494938

Harrison, R. (1964). *Animal machines: The new factory farming industry.* New York: Ballantine Books.

Hay, M., Vulin, A., Génin, S., Sales, P., & Prunier, A. (2003). Assessment of pain induced by castration in piglets: Behavioral and physiological responses over the subsequent 5 days. *Applied Animal Behaviour Science*, *82*, 201–218. doi:10.1016/S0168-1591(03)00059-5

Healey, J. M., Liederman, J., & Geschwind, N. (1986). Handedness is not a unidimensional trait. *Cortex*, *22*, 33–53. doi:10.1016/S0010-9452(86)80031-4

Hengartner, M. P. (2017). The evolutionary life history model of externalizing personality: Bridging human and animal personality science to connect ultimate and proximate mechanisms underlying aggressive dominance, hostility, and impulsive sensation seeking. *Review of General Psychology*, *21*, 330–353. doi:10.1037/gpr0000127

Hengartner, M. P., van der Linden, D., & Dunkel, C. S. (2017). Establishing the substantive interpretation of the GFP by considering evidence from research on personality disorders and animal personality. *Frontiers in Psychology*, *8*, 1–5. doi:10.3389/fpsyg.2017.01771

Henriques, J. B., & Davidson, R. J. (1991). Left frontal hypoactivation in depression. *Journal of Abnormal Psychology*, *100*, 535–545. doi:10.1037/0021-843X.100.4.535

Herculano-Houzel, S. (2011). Brains matter, bodies maybe not: The case for examining neuron numbers irrespective of body size. *Annals of the New York Academy of Sciences*, *1225*, 191–199. doi:10.1111/j.1749-6632.2011.05976.x

Herculano-Houzel, S. (2019). Longevity and sexual maturity vary across species with number of cortical neurons, and humans are no exception. *Journal of Comparative Neurology*, *527*, 1689–1705. doi:10.1002/cne.24564

Herring, S. W. (1976). The dynamics of mastication in pigs. *Archives of Oral Biology*, *21*, 473–480. doi:10.1016/0003-9969(76)90105-9

Herron, M., Martin, J., & Joyce, J. (1978). Quantitative study of the decussating optic axons in the pony, cow, sheep, and pig. *American Journal of Veterinary Research*, *39*, 1137–1139.

Hervé, P.-Y., Zago, L., Petit, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2013). Revisiting human hemispheric specialization with neuroimaging. *Trends in Cognitive Sciences*, *17*, 69–80. doi:10.1016/j.tics.2012.12.004

Hessing, M. J. C., Hagelsø, A. M., van Beek, J. A. M., Wiepkema, P. R., Schouten, W. G. P., & Krukow, R. (1993). Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science*, *37*, 285–295. doi:10.1016/0168-1591(93)90118-9

Hessing, M. J. C., Hagelsø, A. M., Schouten, W. G. P., Wiepkema, P. R., & Van Beek, J. A. M. (1994). Individual behavioral and physiological strategies in pigs. *Physiology & Behavior*, *55*, 39–46. doi:10.1016/0031-9384(94)90007-8

Hicks, R. A., & Pellegrini, R. J. (1978). Handedness and anxiety. *Cortex*, *14*, 119–121. doi:10.1016/S0010-9452(78)80014-8

Highlings-Jackson, J. (1874). On the nature of the duality of the brain. *Brain*, *38*, 80–103.

Holtmann, B., Lagisz, M., & Nakagawa, S. (2017). Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: A meta-analysis. *Functional Ecology*, *31*, 685–696. doi:10.1111/1365-2435.12779

Hook-Costigan, M. A., & Rogers, L. J. (1998). Eye preferences in common marmosets (*Callithrix jacchus*): Influence of age, stimulus, and hand preference. *Laterality: Asymmetries of Body, Brain and Cognition*, *3*, 109–130. doi:10.1080/713754297

Hook, M. A., & Rogers, L. J. (2008). Visuospatial reaching preferences of common marmosets (*Callithrix jacchus*): An assessment of individual biases across a variety of tasks. *Journal of Comparative Psychology*, *122*, 41–51. doi:10.1037/0735-7036.122.1.41

Hopkins, W. D. (1999). On the other hand: Statistical issues in the assessment and interpretation of hand preference data in nonhuman primates. *International Journal of Primatology*, *20*, 851–866. doi:10.1023/a:1020822401195

Hopkins, W. D. (2013). Comparing human and nonhuman primate handedness: Challenges and a modest proposal for consensus. *Developmental Psychobiology*, *55*, 621–636. doi:10.1002/dev.21139

Hopkins, W. D., & Bard, K. A. (1993). Hemispheric specialization in infant chimpanzees (*Pan troglodytes*): Evidence for a relation with gender and arousal. *Developmental Psychobiology*, *26*, 219–235. doi:10.1002/dev.420260405

Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chimpanzees (*Pan*). *Journal of Experimental Psychology: Animal Behavior Processes*, *20*, 413. doi:10.1037/0097-7403.20.4.413

Hopster, H., Van Der Werf, J. T., & Blokhuis, H. J. (1998). Side preference of dairy cows in the milking parlour and its effects on behaviour and heart rate during milking. *Applied Animal Behaviour Science*, *55*, 213–229. doi:10.1016/S0168-1591(97)00064-6

Hughes, A. (1977). The topography of vision in mammals of contrasting life style: Comparative optics and retinal organisation. In F. Crescitelli (Ed.), *The visual system in vertebrates* (pp. 613–756). Springer, Berlin, Heidelberg.

Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics*, *11*, 311–332. doi:doi.org/10.1146/annurev.es.11.110180.001523

Illmann, G., Zachařová, J., Maletínská, J., Stěhulová, I., & Špinka, M. (2002). Nursing behaviour and nursing vocalisations in domestic sows: Repeatability and relationship with maternal investment. *Behaviour*, *139*, 1077–1097. doi:10.1163/15685390260337912

Imfeld-Mueller, S., Wezemael, L. V., Stauffacher, M., Gygax, L., & Hillmann, E. (2011). Do pigs distinguish between situations of different emotional valences during anticipation? *Applied Animal Behaviour Science*, *131*, 86–93. doi:10.1016/j.applanim.2011.02.009

Irving, E., & Brown, C. (2013). Examining the link between personality and laterality in a feral guppy *Poecilia reticulata* population. *Journal of Fish Biology*, *83*, 311–325.

Jackson, C. (2008). When avoidance leads to approach: How ear preference interacts with neuroticism to predict disinhibited approach. *Laterality: Asymmetries of Body, Brain and Cognition*, *13*, 333–373. doi:10.1080/13576500802063053

James, W. (1884). What is an emotion? *Mind*, *9*, 188–205. doi:10 . 1590 / S0100 - 204X2010001100012

Jensen, P. (1993). Nest building in domestic sows: the role of external stimuli. *Animal Behaviour*, *45*, 351–358. doi:10.1006/anbe.1993.1040

Jensen, P. (2002). *The ethology of domestic animals : An introductory text*. New York: CABI.

Jensen, P., Forkman, B., Thodberg, K., & Köster, E. (1995). Individual variation and consistency in piglet behaviour. *Applied Animal Behaviour Science*, *45*, 43–52. doi:10.1016/0168-1591(95)00591-F

John, O. P., & Srivastava, S. (1999). The Big Five trait taxonomy: History, measurement, and theoretical perspectives. In *Handbook of personality: Theory and research* (New York: pp. 102–138).

Jones, S. P. (1989). Neuro-ophthalmology. *British Veterinary Journal*, *145*, 99–120. doi:10 . 1016 / 0007-1935(89)90093-6

Just, C. (2011). A review of literature on the general factor of personality. *Personality and Individual Differences*, *50*, 765–771. doi:10.1016/j.paid.2011.01.008

Kalin, N. H., Larson, C., Shelton, S. E., & Davidson, R. J. (1998). Asymmetric frontal brain activity, cortisol, and behavior associated with fearful temperament in rhesus monkeys. *Behavioral Neuroscience*, *112*, 286–292. doi:10.1037//0735-7044.112.2.286

Kappas, A. (2006). Appraisals are direct, immediate, intuitive, and unwitting... and some are reflective... *Cognition and Emotion*, *20*, 952–975. doi:10.1080/02699930600616080

Kappel, S., Mendl, M., Barrett, D. C., Murrell, J. C., & Whay, H. R. (2017). Lateralized behaviour as indicator of affective state in dairy cows. *Plos One*, *12*, e0184933. doi:10.1371/journal.pone.0184933

Karolis, V., Corbetta, M., & Thiebaut de Schotten, M. (2018). The architecture of functional lateralisation and its relationship to callosal connectivity in the human brain. *Nature Communications*, 1–9. doi:10.1101/372300

Keerthipriya, P., Tewari, R., & Vidya, T. N. C. (2015). Lateralization in trunk and forefoot movements in a population of free-ranging Asian elephants (*Elephas maximus*). *Journal of Comparative Psychology*, *129*, 377–387. doi:10.1037/com0000013

Keiter, D. A., Mayer, J. J., & Beasley, J. C. (2016). What is in a “common” name? A call for consistent terminology for nonnative *Sus scrofa*. *Wildlife Society Bulletin*, *40*, 384–387. doi:10.1002/wsb.649

Kelley, N. J., Hortensius, R., Schutter, D. J. L. G., & Harmon-Jones, E. (2016). The relationship of approach/avoidance motivation and asymmetric frontal cortical activity: A review of studies manipulating frontal asymmetry. *International Journal of Psychophysiology*, *119*, 19–30. doi:10.1016/j.ijpsycho.2017.03.001

Kempermann, G. (2019). Environmental enrichment, new neurons and the neurobiology of individuality. *Nature Reviews Neuroscience*, *20*, 235–245. doi:10.1038/s41583-019-0120-x

Kennis, M., Rademaker, A. R., & Geuze, E. (2013). Neural correlates of personality: An integrative review. *Neuroscience and Biobehavioral Reviews*, *37*, 73–95. doi:10.1016/j.neubiorev.2012.10.012

Kiley-Worthington, M. (1976). The tail movements of ungulates, canids and felids with particular reference to their causation and function as displays. *Behaviour*, *56*, 69–114. doi:10.1163/156853976X00307

Killgore, W. D., & Yurgelun-Todd, D. A. (2007). The right-hemisphere and valence hypotheses: Could they both be right (and sometimes left)? *Social Cognitive and Affective Neuroscience*, *2*, 240–250. doi:10.1093/scan/nsm020

Kinsbourne, M. (1997). Mechanisms and development of cerebral lateralization in children. In C. R. Reynolds & E. Fletcher-Janzen (Eds.), *Handbook of clinical child neuropsychology* (2nd, pp. 102–119). New York: Plenum.

Kleinbeck, S., & McGlone, J. J. (1993). Pig tail posture: A measure of stress. *Texas Technical University Agricultural Science Technical Report T-5-327*, 47–48.

Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Flöel, A., Ringelstein, E. B., & Henningsen, H. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain : A Journal of Neurology*, *123*, 2512–2518. doi:10.1093/brain/123.12.2512

Koboroff, A., Kaplan, G., & Rogers, L. J. (2008). Hemispheric specialization in Australian magpies (*Gymnorhina tibicen*) shown as eye preferences during response to a predator. *Brain Research Bulletin*, *76*, 304–306. doi:10.1016/j.brainresbull.2008.02.015

König von Borstel, U., Pasing, S., & Gauly, M. (2011). Towards a more objective assessment of equine personality using behavioural and physiological observations from performance test training. *Applied Animal Behaviour Science*, *135*, 277–285. doi:10.1016/j.applanim.2011.10.007

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., & Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews*, *23*, 925–935. doi:10.1016/S0149-7634(99)00026-3

Koolhaas, J. M., & van Reenen, C. G. (2016). Animal behavior and well-being symposium: Interaction between coping style/personality, stress, and welfare: Relevance for domestic farm animals. *Journal of Animal Science*, *94*, 2284–2296. doi:10.2527/jas2015-0125

Kornum, B. R., & Knudsen, G. M. (2011). Cognitive testing of pigs (*Sus scrofa*) in translational biobehavioral research. *Neuroscience and Biobehavioral Reviews*, *35*, 437–451. doi:10.1016/j.neubiorev.2010.05.004

Koski, S. E., & Burkart, J. M. (2015). Common marmosets show social plasticity and group-level similarity in personality. *Scientific Reports*, *5*, 8878. doi:10.1038/srep08878

Krause, A., Puppe, B., & Langbein, J. (2017). Coping style modifies general and affective autonomic reactions of domestic pigs in different behavioral contexts. *Frontiers in Behavioral Neuroscience*, *11*, 1–13. doi:10.3389/fnbeh.2017.00103

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*, 394–421. doi:10.1016/j.biopsycho.2010.03.010

Kruska, D. C. T. (1980). Domestikationsbedingte Hirngrößenänderungen bei Säugetieren. *Journal of Zoological Systematics and Evolutionary Research*, *18*, 161–195.

Kruska, D. C. T. (1988). Mammalian domestication and its effect on brain structure and behavior. In *Intelligence and evolutionary biology* (pp. 211–250). Berlin, Heidelberg: Springer.

Kruska, D. C. T. (2005). On the evolutionary significance of encephalization in some eutherian mammals: Effects of adaptive radiation, domestication, and feralization. *Brain, Behavior and Evolution*, *65*, 73–108. doi:10.1159/000082979

Lahey, B. B. (2009). Public health significance of neuroticism. *American Psychologist*, *64*, 241–256. doi:10.1037/a0015309

Lane, A., & Phillips, C. J. C. (2004). A note on behavioural laterality in neonatal lambs. *Applied Animal Behaviour Science*, *86*, 161–167. doi:10.1016/j.applanim.2003.11.015

Langbein, J. (2012). Investigations on training, recall and reversal learning of a Y-maze by dwarf goats (*Capra hircus*): The impact of lateralisation. *Behavioural Processes*, *89*, 304–310. doi:10.1016/j.beproc.2011.12.013

Larose, C., Richard-Yris, M.-A., Hausberger, M., & Rogers, L. J. (2006). Laterality of horses associated with emotionality in novel situations. *Laterality: Asymmetries of Body, Brain and Cognition*, *11*, 355–367. doi:10.1080/13576500600624221

Larsen, J., Berntson, G., Poehlmann, K., Ito, T., & Cacioppo, J. (2008). The psychophysiology of emotion. In M. Lewis, J. Haviland-Jones, & L. Barret (Eds.), *Handbook of emotions* (3rd Edition, Chap. 11, pp. 180–195).

Laska, M. (1998). Laterality in the use of the prehensile tail in the spider monkey (*Ateles geoffroyi*). *Cortex*, *34*, 123–130. doi:10.1016/S0010-9452(08)70741-X

Laska, M., & Tutsch, M. (2000). Laterality of tail resting posture in three species of New World primates. *Neuropsychologia*, *38*, 1040–1046. doi:10.1016/S0028-3932(99)00147-5

Lawrence, A. B., Terlouw, E. M. C., & Illius, A. W. (1991). Individual differences in behavioural responses of pigs exposed to non-social and social challenges. *Applied Animal Behaviour Science*, *30*, 73–86. doi:10.1016/0168-1591(91)90086-d

Lazarus, R. (1993). From psychological stress to the emotions: A history of changing outlooks. *Annual Review of Psychology*, *44*, 1–21. doi:10.1146/annurev.psych.44.1.1

Le Neindre, P., Bernard, E., Boissy, A., Boivin, X., Calandreau, L., Delon, N., Deputte, B., Desmoulin□Canselier, S., Dunier, M., Faivre, N., Giurfa, M., Guichet, J., Lansade, L., Larrère, R., Mormède, P., Prunet, P., Schaal, B., Servière, J., & Terlouw, C. (2017). Animal Consciousness. *EFSA Supporting Publications*, *14*. doi:10.2903/sp.efsa.2017.EN-1196

Leaver, L. A., Ford, S., Miller, C. W., Yeo, M. K., & Fawcett, T. W. (2020). Learning is negatively associated with strength of left / right paw preference in wild grey squirrels (*Sciurus carolinensis*). *Learning & Behavior, in press*. doi:/10.3758/s13420-019-00408-2

Leaver, S. D. A., & Reimchen, T. E. (2008). Behavioural responses of *Canis familiaris* to different tail lengths of a remotely-controlled life-size dog replica. *Behaviour*, *145*, 377–390. doi:10.1163/156853908783402894

Leder, D. (1992). A tale of two bodies : The Cartesian corpse and the lived body. In D. Leder (Ed.), *The body in medical thought and practice* (pp. 17–35). Dordrecht: Springer.

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184. doi:10.1007/978-981-13-3320-0_10

Lee, C., Cafe, L. M., Robinson, S. L., Doyle, R. E., Lea, J. M., Small, A. H., & Colditz, I. G. (2018). Anxiety influences attention bias but not flight speed and crush score in beef cattle. *Applied Animal Behaviour Science*, *205*, 210–215. doi:10.1016/J.APPLANIM.2017.11.003

Lee, C., Verbeek, E., Doyle, R., & Bateson, M. (2016). Attention bias to threat indicates anxiety differences in sheep. *Biology Letters*, *12*, 161–181. doi:10.1098/rsbl.2015.0977

Leliveld, L. M. C. (2019). From science to practice : A review of laterality research on ungulate livestock. *Symmetry*, *11*, 1157. doi:10.3390/sym11091157

Leliveld, L. M. C., Düpjan, S., Tuchscherer, A., & Puppe, B. (2016). Behavioural and physiological measures indicate subtle variations in the emotional valence of young pigs. *Physiology & Behavior*, *157*, 116–124. doi:10.1016/j.physbeh.2016.02.002

Leliveld, L. M. C., Düpjan, S., Tuchscherer, A., & Puppe, B. (2017). Vocal correlates of emotional reactivity within and across contexts in domestic pigs (*Sus scrofa*). *Physiology & Behavior*, *181*, 117–126. doi:10.1016/j.physbeh.2017.09.010

Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science*, *145*, 1–14. doi:10.1016/j.applanim.2013.02.002

Leliveld, L. M. C., Scheumann, M., & Zimmermann, E. (2008). Manual lateralization in early primates: A comparison of two mouse lemur species. *American Journal of Physical Anthropology*, *137*, 156–163. doi:10.1002/ajpa.20852

Leuret, F., & Gratiolet, L. (1839). *Anatomie comparée du système nerveux: considéré dans ses rapports avec l'intelligence*. Paris: Baillière.

Levy, J. (1983). Individual differences in cerebral hemisphere asymmetry: Theoretical issues and experimental considerations. In *Cerebral hemisphere asymmetry: Methods, issues, and implications* (pp. 465–497). New York: Praeger.

Lewis, C. T., & Short, C. (1879). *A latin dictionary founded on the translation of Freund's Latin-German lexicon* (E. Andrews, Ed.). Oxford: Clarendon Press.

Lind, N. M., Moustgaard, A., Jelsing, J., Vajta, G., Cumming, P., & Hansen, A. K. (2007). The use of pigs in neuroscience: Modeling brain disorders. *Neuroscience and Biobehavioral Reviews*, *31*, 728–751. doi:10.1016/j.neubiorev.2007.02.003

Lindell, A. K. (2013). Continuities in emotion lateralization in human and non-human primates. *Frontiers in Human Neuroscience*, *7*, 1–9. doi:10.3389/fnhum.2013.00464

Lindell, A. K. (2018). Lateralization of the expression of facial emotion in humans. In *Progress in brain research* (Vol. 238, pp. 249–270). Elsevier.

Lopes, A. F., Morais, P., Pimentel, M., Rosa, R., Munday, P. L., Gonçalves, E. J., & Faria, A. M. (2016). Behavioural lateralization and shoaling cohesion of fish larvae altered under ocean acidification. *Marine Biology*, *163*, 1–10. doi:10.1007/s00227-016-3026-4

Lorincz, E., & Fabre-Thorpe, M. (1994). Effect of practice on paw preference in a reaching task in cats. *Comptes rendus de l'Académie des sciences Serie III- Sciences de la vie- Life Sciences*, *317*, 1081–1088.

Loyer, C., & Ha, J. (2017). Applications of research in nonhuman animal personality. In J. Vonk, A. Weiss, & S. A. Kuczaj (Eds.), *Personality in nonhuman animals* (Chap. 16, pp. 307–318). Springer.

MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left & right brain. *Scientific American*, *301*, 60–67. doi:10.1038/scientificamerican0709-60

Malkemper, E. P., Painter, M. S., & Landler, L. (2016). Shifted magnetic alignment in vertebrates: Evidence for neural lateralization? *Journal of Theoretical Biology*, *399*, 141–7. doi:10.1016/j.jtbi.2016.03.040

Manning, L., & Thomas-Antérion, C. (2011). Marc Dax and the discovery of the lateralisation of language in the left cerebral hemisphere. *Revue Neurologique*, *167*, 868–872. doi:10.1016/J.NEUROL.2010.10.017

Manteuffel, G., Puppe, B., & Schön, P.-C. C. (2004). Vocalization of farm animals as a measure of welfare. *Applied Animal Behaviour Science*, *88*, 163–182. doi:10.1016/j.applanim.2004.02.012

Marcet Rius, M., Pageat, P., Bienboire-Frosini, C., Teruel, E., Monneret, P., Leclercq, J., Lafont-Lecuelle, C., & Cozzi, A. (2018). Tail and ear movements as possible indicators of emotions in pigs. *Applied Animal Behaviour Science*, *205*, 14–18. doi:10.1016/j.applanim.2018.05.012

Marchant-Forde, A. E. M., & Marchant-Forde, J. N. (2014). Social status and tear staining in nursery pigs. In *ISAE conference book* (p. 145).

Marchant-Forde, J. N. (2002). Piglet- and stockperson-directed sow aggression after farrowing and the relationship with a pre-farrowing, human approach test. *Applied Animal Behaviour Science*, *75*, 115–132. doi:10.1016/s0168-1591(01)00170-8

Marchant, L. F., & McGrew, W. C. (2013). Handedness is more than laterality: Lessons from chimpanzees. *Annals of the New York Academy of Sciences*, *1288*, 1–8. doi:10.1111/nyas.12062

Marr, I., Farmer, K., & Krüger, K. (2018). Evidence for right-sided horses being more optimistic than left-sided horses. *Animals*, *8*, 219. doi:10.3390/ani8120219

Marshall, F. B., Dobney, K., Denham, T., & Capriles, J. M. (2014). Evaluating the roles of directed breeding and gene flow in animal domestication. *Proceedings of the National Academy of Sciences*, *111*, 6153–6158. doi:10.1073/pnas.1312984110

Martin, F., & Niemitz, C. (2003). Right-trunkers and left-trunkers: Side preferences of trunk movements in wild Asian elephants (*Elephas maximus*). *Journal of Comparative Psychology*, *117*, 371–379. doi:10.1037/0735-7036.117.4.371

Mason, G., & Mendl, M. (1993). Why is there no simple way of measuring animal welfare? *Animal Welfare 1993*, *2*, 301–319. doi:10.1002/zoo.20353

Massei, G., & Genov, P. V. (2004). The environmental impact of wild boar. *Galemsy*, *16*, 135–145.

Massen, J. J., Behrens, F., Martin, J. S., Stocker, M., & Brosnan, S. F. (n.d.). A comparative approach to affect and cooperation. *Neuroscience and Biobehavioral Reviews*. doi:10.1016/j.neubiorev.2019.09.027

Maynard Smith, J. (1964). Group selection and kin selection. *Nature*, *201*, 1145–1147. doi:1475-2875-9-181[pii]\n10.1186/1475-2875-9-181

Maynard Smith, J., & Price, G. (1973). The logic of animal conflict. *Nature*, *246*, 15–18. doi:10.1038/246421a0

Mazoyer, B., Zago, L., Jobard, G., Crivello, F., Joliot, M., Perchey, G., Mellet, E., Petit, L., & Tzourio-Mazoyer, N. (2014). Gaussian mixture modeling of hemispheric lateralization for language in a large sample of healthy individuals balanced for handedness. *Plos One*, *9*, 9–14. doi:10.1371/journal.pone.0101165

McCormack, K., Newman, T., Higley, J., Maestripieri, D., & Sanchez, M. (2009). Serotonin transporter gene variation, infant abuse, and responsiveness to stress in rhesus macaque moth-

ers and infants. *Hormones and Behavior*, *55*, 538–547. doi:10.1016/j.yhbeh.2009.01.009. Serotonin

McDowell, L. J., Wells, D. L., Hepper, P. G., & Dempster, M. (2016). Lateral bias and temperament in the domestic cat (*Felis silvestris*). *Journal of Comparative Psychology*, *130*, 313–320. doi:10.1037/com0000030

McElreath, R., & Strimling, P. (2006). How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Animal Behaviour*, *72*, 1135–1139. doi:10.1016/j.anbehav.2006.04.001

McGinley, J. J., & Friedman, B. H. (2015). Autonomic responses to lateralized cold pressor and facial cooling tasks. *Psychophysiology*, *52*, 416–424. doi:10.1111/psyp.12332

McGlone, J. J., Sells, J., Harris, S., & Hurst, R. (1990). Cannibalism in growing pigs: effects of tail docking and housing system on behaviour, performance and immune function. *Technical University Agricultural Science Technical Report T-5-283*, 69–71.

McLeman, M. A., Mendl, M., Jones, R. B., White, R., & Wathes, C. M. (2005). Discrimination of conspecifics by juvenile domestic pigs, *Sus scrofa*. *Animal Behaviour*, *70*, 451–461. doi:10.1016/j.anbehav.2004.11.013

McMillan, F. D. (2000). Quality of life in animals. *Journal of the American Veterinary Medical Association*, *216*, 1904–1910. doi:10.2460/javma.2000.216.1904

Meguerditchian, A., Molesti, S., & Vauclair, J. (2011). Right-handedness predominance in 162 baboons (*Papio anubis*) for gestural communication: consistency across time and groups. *Behavioral Neuroscience*, *125*, 653–660. doi:10.1037/a0023823

Meguerditchian, A., & Vauclair, J. (2006). Baboons communicate with their right hand. *Behavioural Brain Research*, *171*, 170–174. doi:10.1016/j.bbr.2006.03.018

Mehta, P. H., & Prasad, S. (2015). The dual-hormone hypothesis: A brief review and future research agenda. *Current Opinion in Behavioral Sciences*, *3*, 163–168. doi:10.1016/j.cobeha.2015.04.008

Mendl, M., Burman, O. H. P., Parker, R. M. A., & Paul, E. S. (2009). Cognitive bias as an indicator of animal emotion and welfare: Emerging evidence and underlying mechanisms. *Applied Animal Behaviour Science*, *118*, 161–181. doi:10.1016/j.applanim.2009.02.023

Mendl, M., Burman, O. H. P., & Paul, E. S. (2010). An integrative and functional framework for the study of animal emotion and mood. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 2895–2904. doi:10.1098/rspb.2010.0303

Mendl, M., & Paul, E. S. (2020). Assessing affective states in animals. In F. D. McMillan (Ed.), *Mental health and well-being in animals* (2nd, Chap. 23, pp. 328–344). CABI.

Mohr, C., & Bracha, H. S. (2004). Compound measure of hand-foot-eye preference masked opposite turning behavior in healthy right-handers and non-right-handers: Technical comment on Mohr et al. (2003). *Behavioral Neuroscience*, *118*, 1145–1146. doi:10.1037/0735-7044.118.5.1145

Mohr, C., Landis, T., Bracha, H. S., & Brugger, P. (2003). Opposite turning behavior in right-handers and non-right-handers suggests a link between handedness and cerebral dopamine asymmetries. *Behavioral Neuroscience*, *117*, 1448–1452. doi:10.1037/0735-7044.117.6.1448

Molesti, S., Vauclair, J., & Meguerditchian, A. (2016). Hand preferences for unimanual and bimanual coordinated actions in olive baboons (*Papio anubis*): Consistency over time and across populations. *Journal of Comparative Psychology*, *130*, 341–350. doi:10.1037/com0000040

Montag, C., & Panksepp, J. (2017). Primary emotional systems and personality: An evolutionary perspective. *Frontiers in Psychology*, *8*, 1–15. doi:10.3389/fpsyg.2017.00464

Morgante, M., Gianesella, M., Stelletta, C., Versace, E., Cannizzo, C., Ravarotto, L., & Vallortigara, G. (2007). Short-term adaptive response in strongly versus weakly lateralized dairy ewes. *Italian Journal of Animal Science*, *6*, 567–569. doi:10.4081/ijas.2007.1s.567

Morgante, M., Gianesella, M., Versace, E., Contalbrigo, L., Casella, S., Cannizzo, C., Piccione, G., & Stelletta, C. (2010). Preliminary study on metabolic profile of pregnant and non-pregnant ewes with high or low degree of behavioral lateralization. *Animal Science Journal*, *81*, 722–730. doi:10.1111/j.1740-0929.2010.00786.x

Mota, B., Dos Santos, S. E., Ventura-Antunes, L., Jardim-Messeder, D., Neves, K., Kazu, R. S., Noctor, S., Lambert, K., Bertelsen, M. F., Manger, P. R., Sherwood, C. C., Kaas, J. H., & Herculano-Houzel, S. (2019). White matter volume and white/gray matter ratio in mammalian species as a consequence of the universal scaling of cortical folding. *Proceedings of the National Academy of Sciences*, 201716956. doi:10.1073/pnas.1716956116

Müller, G., & Krause, G. (1976). *Theologische Realenzyklopädie*. Berlin: De Gruyter.

Muncer, S. J. (2011). The general factor of personality: Evaluating the evidence from meta-analysis, confirmatory factor analysis and evolutionary theory. *Personality and Individual Differences*, *51*, 775–778. doi:10.1016/j.paid.2011.06.029

Murphy, E., Nordquist, R. E., & van der Staay, F. J. (2014). A review of behavioural methods to study emotion and mood in pigs, *Sus scrofa*. *Applied Animal Behaviour Science*, *159*, 9–28. doi:10.1016/j.applanim.2014.08.002

Musek, J. (2007). A general factor of personality: Evidence for the Big One in the five-factor model. *Journal of Research in Personality*, *41*, 1213–1233. doi:10.1016/j.jrp.2007.02.003

Nawroth, C., Langbein, J., Coulon, M., Gabor, V., Oesterwind, S., Benz-Schwarzburg, J., & von Borell, E. (2019). Farm animal cognition: Linking behaviour, welfare and ethics. *Frontiers in Veterinary Science*, *6*, 24. doi:10.3389/FVETS.2019.00024

Neveu, P. J., & Moya, S. (1997). In the mouse, the corticoid stress response depends on lateralization. *Brain Research*, *749*, 344–346. doi:10.1016/S0006-8993(96)01416-3

Newberry, R. C., & Wood-Gush, D. G. M. (1984). The suckling behaviour of domestic pigs in a semi-natural environment. *Behaviour*, *95*, 11–25. doi:10.1163/156853985X00028

Nieuwenhuis, S., De Geus, E. J., & Aston-Jones, G. (2011). The anatomical and functional relationship between the P3 and autonomic components of the orienting response. *Psychophysiology*, *48*, 162–175. doi:10.1111/j.1469-8986.2010.01057.x

Nilsson, G. E., Dixson, D. L., Domenici, P., McCormick, M. I., Sørensen, C., Watson, S. A., & Munday, P. L. (2012). Near-future carbon dioxide levels alter fish behaviour by interfering with neurotransmitter function. *Nature Climate Change*, *2*, 201–204. doi:10.1038/nclimate1352

Niven, J. E., & Frasnelli, E. (2018). Insights into the evolution of lateralization from the insects. In *Progress in brain research* (Vol. 238, pp. 3–31). Elsevier.

Noonan, G. J., Rand, J. S., Priest, J., Ainscow, J., & Blackshaw, J. K. (1994). Behavioural observations of piglets undergoing tail docking, teeth clipping and ear notching. *Applied Animal Behaviour Science*, *39*, 203–213. doi:10.1016/0168-1591(94)90156-2

Noonan, M., & Axelrod, S. (1989). The stability and intertest consonance of lateral postural-motor biases in rats: results and implications. *Behavioral and Neural Biology*, *52*, 386–405. doi:10.1016/s0163-1047(89)90502-5

O'Malley, C. I., Turner, S. P., D'Eath, R. B., Steibel, J. P., Bates, R. O., Ernst, C. W., & Siegford, J. M. (2019). Animal personality in the management and welfare of pigs. *Applied Animal Behaviour Science*, *218*, 104821. doi:10.1016/j.applanim.2019.06.002

Ocklenburg, S., Korte, S. M., Peterburs, J., Wolf, O. T., & Güntürkün, O. (2016). Stress and laterality – The comparative perspective. *Physiology & Behavior*, *164*, 321–329. doi:10.1016/j.physbeh.2016.06.020

Ocklenburg, S., Packheiser, J., Schmitz, J., Rook, N., Güntürkün, O., Peterburs, J., & Grimshaw, G. M. (2018). Hugs and kisses – The role of motor preferences and emotional lateralization for hemispheric asymmetries in human social touch. *Neuroscience and Biobehavioral Reviews*, *95*, 353–360. doi:10.1016/j.neubiorev.2018.10.007

Ocklenburg, S., Ströckens, F., & Güntürkün, O. (2013). Lateralisation of conspecific vocalisation in non-human vertebrates. *Laterality: Asymmetries of Body, Brain and Cognition*, *18*, 1–31. doi:10.1080/1357650X.2011.626561

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113. doi:10.1016/0028-3932(71)90067-4

Otten, W., Kanitz, E., Tuchscherer, M., Puppe, B., & Nürnberg, G. (2007). Repeated administrations of adrenocorticotropic hormone during gestation in gilts: Effects on growth, behaviour and immune responses of their piglets. *Livestock Science*, *106*, 261–270. doi:10.1016/J.LIVSCI.2006.08.012

Packheiser, J., Rook, N., Dursun, Z., Mesenhöller, J., Wenglorz, A., Güntürkün, O., & Ocklenburg, S. (2019). Embracing your emotions: Affective state impacts lateralisation of human embraces. *Psychological Research*, *83*, 26–36. doi:10.1007/s00426-018-0985-8

Packheiser, J., Schmitz, J., Pan, Y., Basbasse, Y. E., Friedrich, P., Güntürkün, O., & Ocklenburg, S. (2020). Using mobile EEG to investigate alpha and beta asymmetries during hand and foot use. *Frontiers in Neuroscience*, *14*, 1–13. doi:10.3389/fnins.2020.00109

Palmer, A. R. (2004). Symmetry breaking and the evolution of development. *Science*, *306*, 828–833. doi:0.1126/science.1103707

Panksepp, J. (1998). *Affective neuroscience : The foundations of human and animal emotions*. Oxford University Press, USA.

Panksepp, J. (2000). *Emotions as natural kinds within the mammalian brain* (M. Lewis & J. Haviland, Eds.). New York: Guilford Press.

Panksepp, J. (2005). Affective consciousness: Core emotional feelings in animals and humans. *Consciousness and Cognition*, *14*, 30–80. doi:10.1016/j.concog.2004.10.004

Panksepp, J. (2011). The basic emotional circuits of mammalian brains: Do animals have affective lives? *Neuroscience and Biobehavioral Reviews*, *35*, 1791–1804. doi:10.1016/j.neubiorev.2011.08.003

Papadatou-Pastou, M., Martin, M., Munafo, M. R., Ntolka, E., Ocklenburg, S., & Paracchini, S. (2019). The prevalence of left-handedness: Five meta-analyses of 200 studies totaling 2,396,170 individuals. *PsyArXiv Preprints*. doi:10.31234/osf.io/5gjac

Paul, E. S., Harding, E. J., & Mendl, M. (2005). Measuring emotional processes in animals: The utility of a cognitive approach. *Neuroscience and Biobehavioral Reviews*, *29*, 469–491. doi:10.1016/j.neubiorev.2005.01.002

Pedersen, L. J. (2018). Overview of commercial pig production systems and their main welfare challenges. In M. Špinka (Ed.), *Advances in pig welfare* (Chap. 1, pp. 1–26). Elsevier.

Pereira, L. C., Duarte, R. B., Maior, R. S., & Barros, M. (2018). Natural predator and a human stimulus differently affect the behavior, cortisol and cerebral hemisphere activity of marmoset monkeys. *Physiology & Behavior*, *195*, 112–117. doi:10.1016/j.physbeh.2018.07.027

Perez, D. M., Heatwole, S. J., Morrell, L. J., & Backwell, P. R. Y. (2015). Handedness in fiddler crab fights. *Animal Behaviour*, *110*, 99–104. doi:10.1016/j.anbehav.2015.09.012

Phillips, C. J. C., Llewellyn, S., & Claudia, A. (2003). Laterality in bovine behavior in an extensive partially suckled herd and an intensive dairy herd. *Journal of Dairy Science*, *86*, 3167–3173. doi:10.3168/jds.S0022-0302(03)73919-8

Phillips, C. J. C., Oevermans, H., Syrett, K. L., Jespersen, A. Y., & Pearce, G. P. (2015). Lateralization of behavior in dairy cows in response to conspecifics and novel persons. *Journal of Dairy Science*, *98*, 2389–400. doi:10.3168/jds.2014-8648

Pollet, T. V., Stulp, G., & Groothuis, T. G. G. (2013). Born to win? Testing the fighting hypothesis in realistic fights: Left-handedness in the ultimate fighting championship. *Animal Behaviour*, *86*, 839–843. doi:10.1016/j.anbehav.2013.07.026

Porcher, J. (2014). *Vivre avec les animaux: Une utopie pour le XXIe siècle* (La Découve). La Découverte.

Porges, S. W. (1995). Orienting in a defensive world: Mammalian modifications of our evolutionary heritage. A polyvagal theory. *Psychophysiology*, *32*, 301–318. doi:10.1111/j.1469-8986.1995.tb01213.x. arXiv: 1110.0284v1

Pourtois, G., Schettino, A., & Vuilleumier, P. (2013). Brain mechanisms for emotional influences on perception and attention: What is magic and what is not. *Biological Psychology*, *92*, 492–512. doi:10.1016/j.biopsycho.2012.02.007

Pradeu, T. (2016). The many faces of biological individuality. *Biology and Philosophy*, *31*, 761–773. doi:10.1007/s10539-016-9553-z

Prelle, I., Phillips, C. J. C., Paranhos Da Costa, M. J., Vandenberghe, N. C., & Broom, D. M. (2004). Are cows that consistently enter the same side of a two-sided milking parlour more fearful of novel situations or more competitive? *Applied Animal Behaviour Science*, *87*, 193–203. doi:10.1016/j.applanim.2004.01.014

Preston, C. J. (2010). *Grounding knowledge: Environmental philosophy, epistemology, and place*. University of Georgia Press.

Prete, G., Laeng, B., Fabri, M., Foschi, N., & Tommasi, L. (2015). Right hemisphere or valence hypothesis, or both? The processing of hybrid faces in the intact and callosotomized brain. *Neuropsychologia*, *68*, 94–106. doi:10.1016/j.neuropsychologia.2015.01.002

Prieur, J., Pika, S., Barbu, S., & Blois-Heulin, C. (2016). A multifactorial investigation of captive chimpanzees' intraspecific gestural laterality. *Animal Behaviour*, *116*, 31–43. doi:10.1016/j.anbehav.2016.03.024

Prunier, A., Averos, X., Dimitrov, I., Edwards, S. A., Hillmann, E., Holinger, M., Ilieski, V., Leming, R., Tallet, C., Turner, S. P., Zupan, M., & Camerlink, I. (2020). Review: Early life predisposing factors for biting in pigs. *Animal*, *14*, 570–587. doi:10.1017/S1751731119001940

Pujol, J., Deus, J., Losilla, J. M., & Capdevila, A. (1999). Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology*, *52*, 1038–1043. doi:10.1212/WNL.52.5.1038

Puppe, B., Zebunke, M., Düpjan, S., & Langbein, J. (2012). Kognitiv-emotionale Umweltbewältigung beim Hausschwein -Herausforderung für Tierhaltung und Tierschutz. *Züchtungskunde*, *84*, 307–319.

Quaranta, A., Siniscalchi, M., Frate, A., Iacoviello, R., Buonavoglia, C., & Vallortigara, G. (2006). Lateralised behaviour and immune response in dogs: Relations between paw preference and interferon-gamma, interleukin-10 and IgG antibodies production. *Behavioural Brain Research*, *166*, 236–40. doi:10.1016/j.bbr.2005.08.001

Quaranta, A., Siniscalchi, M., & Vallortigara, G. (2007). Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology*, *17*, R199–R201. doi:10.1016/j.cub.2007.02.008

Quaranta, A., Siniscalchi, M., Albrizio, M., Volpe, S., Buonavoglia, C., & Vallortigara, G. (2008). Influence of behavioural lateralization on interleukin-2 and interleukin-6 gene expression in dogs before and after immunization with rabies vaccine. *Behavioural Brain Research*, *186*, 256–60. doi:10.1016/j.bbr.2007.08.014

Racca, A., Guo, K., Meints, K., & Mills, D. S. (2012). Reading faces: Differential lateral gaze bias in processing canine and human facial expressions in dogs and 4-year-old children. *Plos One*, *7*, 1–10. doi:10.1371/journal.pone.0036076

Raoult, C., & Gygax, L. (2018). Valence and intensity of video stimuli of dogs and conspecifics in sheep: Approach-avoidance, operant response, and attention. *Animals*, *8*, 121. doi:10.3390/ani8070121

Raoult, C., & Gygax, L. (2019). Mood induction alters attention toward negative-positive stimulus pairs in sheep. *Scientific Reports*, *9*, 7759. doi:10.1038/s41598-019-44330-z

Rattenborg, N. C., Martinez-Gonzalez, D., & Lesku, J. A. (2009). Avian sleep homeostasis: Convergent evolution of complex brains, cognition and sleep functions in mammals and birds. *Neuroscience and Biobehavioral Reviews*, *33*, 253–270. doi:10.1016/j.neubiorev.2008.08.010

Rault, J.-L., Truong, S., Hemsworth, L., Le Chevoir, M., Bauquier, S., & Lai, A. (2019). Gentle abdominal stroking ('belly rubbing') of pigs by a human reduces EEG total power and increases EEG frequencies. *Behavioural Brain Research*, *374*, 111892. doi:10.1016/j.bbr.2019.04.006

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*, 291–318. doi:10.1111/j.1469-185X.2007.00010.x

Reddon, A. R., & Hurd, P. L. (2008). Aggression, sex and individual differences in cerebral lateralization in a cichlid fish. *Biology Letters*, *4*, 338–340. doi:10.1098/rsbl.2008.0206

Reddon, A. R., & Hurd, P. L. (2009a). Individual differences in cerebral lateralization are associated with shy-bold variation in the convict cichlid. *Animal Behaviour*, *77*, 189–193. doi:10.1016/j.anbehav.2008.09.026

Reddon, A. R., & Hurd, P. L. (2009b). Sex differences in the cerebral lateralization of a cichlid fish when detouring to view emotionally conditioned stimuli. *Behavioural Processes*, *82*, 25–29. doi:10.1016/j.beproc.2009.03.005

Reefmann, N., Bütikofer Kaszàs, F., Wechsler, B., & Gygax, L. (2009a). Ear and tail postures as indicators of emotional valence in sheep. *Applied Animal Behaviour Science*, *118*, 199–207. doi:10.1016/j.applanim.2009.02.013

Reefmann, N., Bütikofer Kaszàs, F., Wechsler, B., & Gygax, L. (2009b). Physiological expression of emotional reactions in sheep. *Physiology & Behavior*, *98*, 235–241. doi:10.1016/j.physbeh.2009.05.017

Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2014). Social support in pigs with different coping styles. *Physiology & Behavior*, *129*, 221–229. doi:10.1016/j.physbeh.2014.02.059

Reimert, I., Bolhuis, J. E., Kemp, B., & Rodenburg, T. B. (2013). Indicators of positive and negative emotions and emotional contagion in pigs. *Physiology & Behavior*, *109*, 42–50. doi:10.1016/j.physbeh.2012.11.002

Reimert, I., Fong, S., Rodenburg, T. B., & Bolhuis, J. E. (2017). Emotional states and emotional contagion in pigs after exposure to a positive and negative treatment. *Applied Animal Behaviour Science*, *193*, 37–42. doi:10.1016/j.applanim.2017.03.009

Reisenzein, R., & Weber, H. (2009). Personality and emotion. In P. J. Corr & G. Matthews (Eds.), *The Cambridge handbook of personality psychology* (pp. 54–71). Cambridge University Press.

Reiss, M., & Reiss, G. (2002). Tonguedness in cats. *Perceptual and Motor Skills*, *94*, 152. doi:10.2466/pms.2002.94.1.152

Reznik, S. J., & Allen, J. J. B. (2018). Frontal asymmetry as a mediator and moderator of emotion: An updated review. *Psychophysiology*, *55*, e12965. doi:10.1111/psyp.12965

Richter, S. H., & Hintze, S. (2019). From the individual to the population–and back again? Emphasising the role of the individual in animal welfare science. *Applied Animal Behaviour Science*, *212*, 1–8. doi:10.1016/j.applanim.2018.12.012

Riedstra, B., & Groothuis, T. G. (2004). Prenatal light exposure affects early feather-pecking behaviour in the domestic chick. *Animal Behaviour*, *67*, 1037–1042. doi:10.1016/j.anbehav.2003.10.009

Rizhova, L. Y., & Kokorina, E. P. (2005). Behavioural asymmetry is involved in regulation of autonomic processes: Left side presentation of food improves reproduction and lactation in cows. *Behavioural Brain Research*, *161*, 75–81. doi:10.1016/j.bbr.2005.01.007

Roberts, K., Hemmings, A. J., Moore-Colyer, M., Parker, M. O., & McBride, S. D. (2016). Neural modulators of temperament: A multivariate approach to personality trait identification in the horse. *Physiology & Behavior*, *167*, 125–131. doi:10.1016/j.physbeh.2016.08.029

Robins, A., Berthoux, G., Santurtun, E., Navarro, G., & Phillips, C. J. C. (2019). Sheep quickstep while the floor rock and rolls: Visuomotor lateralization during simulated sea travel. *Animals*, *9*, 700.

Robins, A., Goma, A. A., Ouine, L., & Phillips, C. J. C. (2018). The eyes have it: Lateralized coping strategies in cattle herds responding to human approach. *Animal Cognition*, *21*, 685–702. doi:10.1007/s10071-018-1203-1

Robins, A., Lippolis, G., Bisazza, A., Vallortigara, G., & Rogers, L. J. (1998). Lateralized agonistic responses and hindlimb use in toads. *Animal Behaviour*, *56*, 875–881. doi:10.1006/anbe.1998.0877

Robins, A., & Phillips, C. J. C. (2010). Lateralised visual processing in domestic cattle herds responding to novel and familiar stimuli. *Laterality: Asymmetries of Body, Brain and Cognition*, *15*, 514–534. doi:10.1080/13576500903049324

Rochais, C., Sébilleau, M., Menoret, M., Oger, M., Henry, S., Hausberger, M., & Cousillas, H. (2018). Attentional state and brain processes: State-dependent lateralization of EEG profiles in horses. *Scientific Reports*, *8*, 1–7. doi:10.1038/s41598-018-28334-9

Roche, D. G., Careau, V., & Binning, S. A. (2016). Demystifying animal 'personality' (or not): Why individual variation matters to experimental biologists. *The Journal of Experimental Biology*, *219*, 3832–3843. doi:10.1242/jeb.146712

Rogers, L. J. (1990). Light input and the reversal of functional lateralization in the chicken brain. *Behavioural Brain Research*, *38*, 211–221. doi:10.1016/0166-4328(90)90176-f

Rogers, L. J. (2009). Hand and paw preferences in relation to the lateralized brain. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 943–954. doi:10.1098/rstb.2008.0225

Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science*, *127*, 1–11. doi:10.1016/j.applanim.2010.06.008

Rogers, L. J. (2011). Does brain lateralization have practical implications for improving animal welfare? *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, *6*, 1–10. doi:10.1079/PAVSNNR20116036

Rogers, L. J. (2017a). A matter of degree: Strength of brain asymmetry and behaviour. *Symmetry*, *9*, 57. doi:10.3390/sym9040057

Rogers, L. J. (2017b). Eye and ear preferences. *Neuromethods*, *122*, 79–102. doi:10.1007/978-1-4939-6725-4_3

Rogers, L. J. (2018). Manual bias, behavior, and cognition in common marmosets and other primates. In *Progress in brain research* (Vol. 238, pp. 91–113). Elsevier.

Rogers, L. J., & Andrew, R. J. (2002). *Comparative vertebrate lateralization*. Cambridge University Press.

Rogers, L. J., & Anson, J. M. (1979). Lateralisation of function in the chicken fore-brain. *Pharmacology, Biochemistry and Behavior*, *10*, 679–686. doi:10.1016/0091-3057(79)90320-4

Rogers, L. J., & Kaplan, G. (2019). Does functional lateralization in birds have any implications for their welfare ? *Symmetry*, *11*, 1043. doi:10.3390/sym9040057

Rogers, L. J., & Vallortigara, G. (2015). When and why did brains break symmetry? *Symmetry*, *7*, 2181–2194. doi:10.3390/sym7042062

Rogers, L. J., & Vallortigara, G. (2019). Complementary specializations of the left and right sides of the honeybee brain. *Frontiers in Psychology*, *10*, 280. doi:10.3389/fpsyg.2019.00280

Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided brains : The biology and behaviour of brain asymmetries*. Cambridge, U.K.: Cambridge University Press.

Rogers, L. J., Ward, J. P., & Stafford, D. (1994). Eye dominance in the small-eared bush-baby, *Otolemur garnettii*. *Neuropsychologia*, *32*, 257–264. doi:10.1016/0028-3932(94)90011-6

Rogers, L. J., & Workman, L. (1989). Light exposure during incubation affects competitive behaviour in domestic chicks. *Applied Animal Behaviour Science*, *23*, 187–198. doi:10.1016/0168-1591(89)90109-3

Rogers, L. J., Zucca, P., & Vallortigara, G. (2004). Advantages of having a lateralized brain. *Proceedings of the Royal Society B-Biological Sciences*, *271*, 420–422. doi:10.1098/rsbl.2004.0200

Root-Bernstein, M., Narayan, T., Cornier, L., & Bourgeois, A. (2019). Context-specific tool use by *Sus cebifrons*. *Mammalian Biology*, *98*, 102–110. doi:10.1016/J.MAMBIO.2019.08.003

Rosa-Salva, O., Regolin, L., Mascalzoni, E., & Vallortigara, G. (2012). Cerebral and behavioural asymmetries in animal social recognition. *Comparative Cognition & Behavior Reviews*, *7*, 110–138. doi:10.3819/ccbr.2012.70006

Rosen, G. D., Berrebi, A. S., Yutzey, D. A., & Denenberg, V. H. (1983). Prenatal testosterone causes shift of asymmetry in neonatal tail posture of the rat. *Developmental Brain Research*, *9*, 99–101. doi:10.1016/0165-3806(83)90114-1

Rosen, G. D., Finklestein, S., Stoll, A. L., Yutzey, D. A., & Denenberg, V. H. (1984). Neonatal tail posture and its relationship to striatal dopamine asymmetry in the rat. *Brain Research*, *297*, 305–308. doi:10.1016/0006-8993(84)90571-7

Ross, D. A., Glick, S. D., & Meibach, R. C. (1981). Sexually dimorphic brain and behavioral asymmetries in the neonatal rat. *Proceedings of the National Academy of Sciences of the United States of America*, *78*, 1958–61. doi:10.1073/pnas.78.3.1958

Rousseau, J.-J. (1754). *Discours sur l'origine et les fondements de l'inégalité parmi les hommes*.

Ruis, M. A. W., De Groot, J., Te Brake, J. H., Dinand Ekkel, E., Van de Burgwal, J. A., Erkens, J. H., Engel, B., Buist, W. G., Blokhuis, H. J., & Koolhaas, J. M. (2001). Behavioural and physiological consequences of acute social defeat in growing gilts: Effects of the social environment. *Applied Animal Behaviour Science*, *70*, 201–225. doi:10.1016/S0168-1591(00)00150-7

Ruis, M. A. W., Te Brake, J. H. a., Engel, B., Buist, W. G., Blokhuis, H. J., & Koolhaas, J. M. (2002). Implications of coping characteristics and social status for welfare and production of paired growing gilts. *Applied Animal Behaviour Science*, *75*, 207–231. doi:10.1016/S0168-1591(01)00191-5

Ruis, M. A. W., Te Brake, J. H. A., van de Burgwal, J. A., de Jong, I. C., Blokhuis, H. J., & Koolhaas, J. M. (2000). Personalities in female domesticated pigs: Behavioural and physiological indications. *Applied Animal Behaviour Science*, *66*, 31–47. doi:10.1016/S0168-1591(99)00070-2

Russell, J. A. (2003). Core affect and the psychological construction of emotion. *Psychological Review*, *110*, 145–172. doi:10.1037/0033-295X.110.1.145

Russell, J. A., & Barrett, L. F. (1999). Core affect, prototypical emotional episodes, and other things called emotion: Dissecting the elephant. *Journal of Personality and Social Psychology*, *76*, 805–819. doi:10.1037//0022-3514.76.5.805

Sambraus, H., & Steiger, A. (1997). *Das Buch vom Tierschutz*. Stuttgart: Ferdinand Enke.

Sander, D., Grandjean, D., Pourtois, G., Schwartz, S., Seghier, M. L., Scherer, K. R., & Vuilleumier, P. (2005). Emotion and attention interactions in social cognition: Brain regions involved in processing anger prosody. *NeuroImage*, *28*, 848–858. doi:10.1016/j.neuroimage.2005.06.023

Sandoe, P., & Simonsen, H. B. (1992). Assessing animal welfare: Where does science end and philosophy begin? *Animal Welfare*, *1*, 257–267.

Sanson, A. (1907). *Traité de zootechnie. Tome 1* (Librairie).

Sauleau, P., Lapouble, E., Val-Laillet, D., & Malbert, C.-H. (2009). The pig model in brain imaging and neurosurgery. *Animal*, *3*, 1138–1151. doi:10.1017/S1751731109004649

Savage, R., & Eysenck, H. (1964). The definition and measurement of emotionality. In H. Eysenck (Ed.), *Experiments in motivation* (pp. 292–314). Oxford: Pergamon Press.

Schachter, S., & Singer, J. (1962). Cognitive, social, and physiological determinants of emotional state. *Psychological Review*, *69*, 379–399. doi:10.1037/h0046234

Schaffer, C. E., Davidson, R. J., & Saron, C. (1983). Frontal and parietal electroencephalogram asymmetry in depressed and nondepressed subjects. *Biological Psychiatry*, *18*, 753–62.

Schepman, A., Rodway, P., & Pritchard, H. (2016). Right-lateralized unconscious, but not conscious, processing of affective environmental sounds. *Laterality: Asymmetries of Body, Brain and Cognition*, *21*, 606–632. doi:10.1080/1357650X.2015.1105245

Scherer, K. R., & Moors, A. (2019). The emotion process: Event appraisal and component differentiation. *Annual Review of Psychology*, *70*, 719–745. doi:10.1146/annurev-psych-122216-011854

Scherer, K. R., Schorr, A., & Johnstone, T. (2001). *Appraisal processes in emotion: Theory, methods, research*. Oxford University Press.

Schneider, L. A., Delfabbro, P. H., & Burns, N. R. (2013). Temperament and lateralization in the domestic dog (*Canis familiaris*). *Journal of Veterinary Behavior: Clinical Applications and Research*, *8*, 124–134. doi:10.1016/j.jveb.2012.06.004

Schnell, A. K., Jozet-Alves, C., Hall, K. C., Radday, L., & Hanlon, R. T. (2019). Fighting and mating success in giant Australian cuttlefish is influenced by behavioural lateralization. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20182507. doi:10.1098/rspb.2018.2507

Schuetz, A., Farmer, K., & Krueger, K. (2017). Social learning across species: horses (*Equus caballus*) learn from humans by observation. *Animal Cognition*, *20*, 567–573. doi:10.1007/s10071-016-1060-8

Schwartz, G. E., Ahern, G. L., & Brown, S.-L. (1979). Lateralized facial muscle response to positive and negative emotional stimuli. *Psychophysiology*, *16*, 561–571. doi:10.1111/j.1469-8986.1979.tb01521.x

Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *The American Naturalist*, *139*, 1052–1069. doi:10.1086/285372

Sih, A., Bell, A. M., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *The Quarterly Review of Biology*, *79*, 241–277. doi:10.1086/516403

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2762–2772. doi:10.1098/rstb.2012.0216

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state-behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, *30*, 50–60. doi:10.1016/j.tree.2014.11.004

Silva, P. A., Trigo, S., Marques, C. I., Cardoso, G. C., & Marta, C. (2020). Experimental evidence for a role of dopamine on avian personality traits. *Journal of Experimental Biology, in press*. doi:10.1242/jeb.216499

Siniscalchi, M. (2017). Olfactory Lateralization. In *Lateralized brain functions* (pp. 103–120). Humana Press, New York, NY.

Siniscalchi, M., Bertino, D., D'Ingeo, S., & Quaranta, A. (2019). Relationship between motor laterality and aggressive behavior in sheepdogs. *Symmetry*, *11*, 233. doi:10.3390/sym11020233

Siniscalchi, M., Laddago, S., & Quaranta, A. (2016). Auditory lateralization of conspecific and heterospecific vocalizations in cats. *Laterality: Asymmetries of Body, Brain and Cognition*, *21*, 215–227. doi:10.1080/1357650X.2015.1116541

Siniscalchi, M., Lusito, R., Vallortigara, G., & Quaranta, A. (2013). Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. *Current Biology*, *23*, 2279–2282. doi:10.1016/j.cub.2013.09.027

Siniscalchi, M., Padalino, B., Lusito, R., & Quaranta, A. (2014). Is the left forelimb preference indicative of a stressful situation in horses? *Behavioural Processes*, *107*, 61–7. doi:10.1016/j.beproc.2014.07.018

Siniscalchi, M., Quaranta, A., & Rogers, L. J. (2008). Hemispheric specialization in dogs for processing different acoustic stimuli. *Plos One*, *3*, e3349. doi:10.1371/journal.pone.0003349

Siniscalchi, M., Sasso, R., Pepe, A. M., Dimatteo, S., Vallortigara, G., & Quaranta, A. (2011). Sniffing with the right nostril: Lateralization of response to odour stimuli by dogs. *Animal Behaviour*, *82*, 399–404. doi:10.1016/j.anbehav.2011.05.020

Siniscalchi, M., Sasso, R., Pepe, A. M., Vallortigara, G., & Quaranta, A. (2010). Dogs turn left to emotional stimuli. *Behavioural Brain Research*, *208*, 516–521. doi:10.1016/j.bbr.2009.12.042

Smith, A. V., Proops, L., Grounds, K., Wathan, J., & McComb, K. (2016). Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). *Biology Letters*, *12*, 20150907. doi:10.1098/rsbl.2015.0907

Sokolov, E., Spinks, J., Näätänen, R., & Lyytinen, H. (2002). *The Orienting Response in Information Processing*. London: Lawrence Erlbaum Associates.

Sommer, V., Lowe, A., & Dietrich, T. (2016). Not eating like a pig: European wild boar wash their food. *Animal Cognition*, *19*, 245–249. doi:10.1007/s10071-015-0903-z

Spocter, M. A., Uddin, A., Ng, J. C., Wong, E., Wang, V. X., Tang, C., Wicinski, B., Haas, J., Bitterman, K., Raghanti, M. A., Dunn, R., Hof, P. R., Sherwood, C. C., Jovanovik, J., Rusbridge, C., & Manger, P. R. (2018). Scaling of the corpus callosum in wild and domestic canids: Insights into the domesticated brain. *Journal of Comparative Neurology*, *526*, 2341–2359. doi:10.1002/cne.24486

Spoolder, H. A. M., Burbidge, J. A., Lawrence, A. B., Simmins, P. H., & Edwards, S. A. (1996). Individual behavioural differences in pigs: Intra-and inter-test consistency. *Applied Animal Behaviour Science*, *49*, 185–198. doi:10.1016/0168-1591(96)01033-7

Staddon, J. (1989). Animal psychology: The tyranny of anthropocentrism. In P. P. G. Klopfer & P. H. Bateson (Eds.), *Perspectives in ethology, Vol. 8. Whither ethology?* (pp. 123–135). Plenum Press.

Statham, P., Green, L., Bichard, M., & Mendl, M. (2009). Predicting tail-biting from behaviour of pigs prior to outbreaks. *Applied Animal Behaviour Science*, *121*, 157–164. doi:10.1016/j.applanim.2009.09.011

Steenhuis, R., & Bryden, M. (1989). Different dimensions of hand preference that relate to skilled and unskilled activities. *Cortex*, *25*, 289–304. doi:10.1016/S0010-9452(89)80044-9

Stevens, N. J., Wright, K. A., Covert, H. H., & Nadler, T. (2008). Tail postures of four quadrupedal leaf monkeys (*Pygathrix nemaeus*, *P. cinerea*, *Trachypithecus delacouri* and *T. hatinhensis*) at the endangered primate rescue center, Cuc Phuong National Park, Vietnam. *Vietnamese Journal of Primatology*, *2*, 13–24. doi:10.1007/s10764-008-9319-9

Stolba, A., & Wood-Gush, D. G. (1984). The identification of behavioural key features and their incorporation into a housing design for pigs. *Annales de recherches vétérinaires. Annals of veterinary research*, *15*, 287–299.

Stolba, A., & Wood-Gush, D. G. M. (1989). The behaviour of pigs in a semi-natural environment. *Animal Science*, *48*, 419–425. doi:10.1017/S0003356100040411

Stracke, J., Otten, W., Tuchscherer, A., Puppe, B., & Düpjan, S. (2017). Serotonin depletion induces pessimistic-like behavior in a cognitive bias paradigm in pigs. *Physiology & Behavior*, *174*, 18–26. doi:10.1016/j.physbeh.2017.02.036

Ströckens, F., Güntürkün, O., & Ocklenburg, S. (2013). Limb preferences in non-human vertebrates. *Laterality: Asymmetries of Body, Brain and Cognition*, *18*, 536–575. doi:10 . 1080 / 1357650x.2012.723008

Sullivan, R. M., Chehab, S. L., Dufresne, M. M., & Laplante, F. (2012). Role of sex in the neurochemical and neuroendocrine correlates of paw preference in the rat. *Neuroscience*, *202*, 192–201. doi:10.1016/j.neuroscience.2011.12.001

Sutherland, M. A., Niekamp, S. R., Rodriguez-Zas, S. L., & Salak-Johnson, J. L. (2006). Impacts of chronic stress and social status on various physiological and performance measures in pigs of different breeds. *Journal of Animal Science*, *84*, 588–596. doi:10.2527/2006.843588x

Sutherland, M. A., & Tucker, C. B. (2011). The long and short of it: A review of tail docking in farm animals. *Applied Animal Behaviour Science*, *135*, 179–191. doi:10.1016/j.applanim.2011.10.015

Sutton, S. K., & Davidson, R. J. (1997). Prefrontal brain asymmetry: A biological substrate of the behavioral approach and inhibition systems. *Psychological Science*, *8*, 204–210. doi:10.1111/j.1467-9280.1997.tb00413.x

Swindle, M. M., & Smith, A. C. (2008). Swine in biomedical research. In *Sourcebook of models for biomedical research* (pp. 233–239). Totowa, NJ: Humana Press.

Tallet, C., Brajon, S., Devillers, N., & Lensink, J. (2018). Pig-human interactions: Creating a positive perception of humans to ensure pig welfare. In M. Špinka (Ed.), *Advances in pig welfare* (Chap. 13, pp. 381–398). Elsevier.

Telkänranta, H., Marchant-Forde, J. N., & Valros, A. (2016). Tear staining in pigs: A potential tool for welfare assessment on commercial farms. *Animal*, *10*, 318–325. doi:10 . 1017 / S175173111500172X

Terburg, D., Morgan, B., & van Honk, J. (2009). The testosterone-cortisol ratio: A hormonal marker for proneness to social aggression. *International Journal of Law and Psychiatry*, *32*, 216–223. doi:10.1016/j.ijlp.2009.04.008

Thompson, E. (1851). *The passions of animals* (Bradbury A). London.

Tomassetti, D., Caracciolo, S., Manciocco, A., Chiarotti, F., Vitale, A., & De Filippis, B. (2019). Personality and lateralization in common marmosets (*Callithrix jacchus*). *Behavioural Processes*, *167*, 103899. doi:10.1016/j.beproc.2019.103899

Tomkins, L. M., McGreevy, P. D., & Branson, N. J. (2010a). Lack of standardization in reporting motor laterality in the domestic dog (*Canis familiaris*). *Journal of Veterinary Behavior: Clinical Applications and Research*, *5*, 235–239. doi:10.1016/j.jveb.2010.03.002

Tomkins, L. M., Thomson, P. C., & McGreevy, P. D. (2010b). First-stepping Test as a measure of motor laterality in dogs (*Canis familiaris*). *Journal of Veterinary Behavior*, *5*, 247–255. doi:10.1016/j.jveb.2010.03.001

Tops, M., Quirin, M., Boksem, M. A. S., & Koole, S. L. (2017). Large-scale neural networks and the lateralization of motivation and emotion. *International Journal of Psychophysiology*, *119*, 41–49. doi:10.1016/j.ijpsycho.2017.02.004

Tran, U. S., Stieger, S., & Voracek, M. (2014). Evidence for general right-, mixed-, and left-sidedness in self-reported handedness, footedness, eyedness, and earedness, and a primacy of footedness in a large-sample latent variable analysis. *Neuropsychologia*, *62*, 220–232. doi:10.1016/j.neuropsychologia.2014.07.027

Tran, U. S., Stieger, S., & Voracek, M. (2015). Mixed-footedness is a more relevant predictor of schizotypy than mixed-handedness. *Psychiatry Research*, *225*, 446–451. doi:10.1016/j.psychres.2014.11.069

Tran, U. S., & Voracek, M. (2016). Footedness is associated with self-reported sporting performance and motor abilities in the general population. *Frontiers in Psychology*, *7*, 1–12. doi:10.3389/fpsyg.2016.01199

Trut, L. N. (1999). Early canid domestication: The farm-fox experiment: Foxes bred for tamability in a 40-year experiment exhibit remarkable transformations that suggest an interplay between behavioral genetics and development. *American Scientist*, *87*, 160–169. doi:10.2307/27857815

Trut, L. N., Oskina, I., & Kharlamova, A. (2009). Animal evolution during domestication: The domesticated fox as a model. *Bioessays*, *31*, 349–360. doi:10.1002/bies.200800070.Animal

Tsuchiya, N., Wilke, M., Frässle, S., & Lamme, V. A. (2015). No-report paradigms: Extracting the true neural correlates of consciousness. *Trends in Cognitive Sciences*, *19*, 757–770. doi:10.1016/j.tics.2015.10.002. arXiv: arXiv:1011.1669v3

Turner, S. P., Camerlink, I., Baxter, E. M., Eath, R. B. D., Desire, S., & Roehe, R. (2018). Breeding for pig welfare: Opportunities and challenges. In M. Špinka (Ed.), *Advances in pig welfare* (Chap. 14, pp. 399–414). Elsevier.

Tzourio-Mazoyer, N., Petit, L., Zago, L., Crivello, F., Vinuesa, N., Joliot, M., Jobard, G., Mellet, E., & Mazoyer, B. (2015). Between-hand difference in ipsilateral deactivation is associated with hand lateralization: fMRI mapping of 284 volunteers balanced for handedness. *Frontiers in Human Neuroscience*, *9*, 1–12. doi:10.3389/fnhum.2015.00005

Uomini, N. T., & Hunt, G. R. (2016). Multidimensional laterality in new caledonian crows. In *Proceedings of the 5th North Sea Laterality Meeting*, Groningen, The Netherlands.

Vallortigara, G. (2000). Comparative neuropsychology of the dual brain: A stroll through animals' left and right perceptual worlds. *Brain and Language*, *73*, 189–219. doi:10.1006/brln.2000.2303

Vallortigara, G. (2006). The evolutionary psychology of left and right: Costs and benefits of lateralization. *Developmental Psychobiology*, *48*, 418–427. doi:10.1002/dev.20166

Vallortigara, G. (2019). Giorgio Vallortigara. *Current Biology*, *29*, R606–R608. doi:10.1016/j.cub.2019.05.039

Vallortigara, G., Regolin, L., & Pagni, P. (1999). Detour behaviour, imprinting and visual lateralization in the domestic chick. *Cognitive Brain Research*, *7*, 307–320. doi:10.1016/S0926-6410(98)00033-0

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences*, *28*, 575–588. doi:10.1017/S0140525X05000105

Vallortigara, G., & Versace, E. (2017). Laterality at the neural, cognitive, and behavioral levels. In *APA handbook of comparative psychology: Basic concepts, methods, neural substrate, and behavior.* (pp. 557–577). doi:10.1037/0000011-027

Valros, A. (2018). Tail biting. In M. Špinka (Ed.), *Advances in pig welfare* (Chap. 5, pp. 137–166). Elsevier.

Valros, A., & Heinonen, M. (2015). Save the pig tail. *Porcine Health Management*, *1*, 2. doi:10.1186/2055-5660-1-2

van den Berg, F. E., Swinnen, S. P., & Wenderoth, N. (2011). Involvement of the primary motor cortex in controlling movements executed with the ipsilateral hand differs between left- and right-handers. *Journal of Cognitive Neuroscience*, *23*, 3456–3469. doi:10.1162/jocn_a_00018

van der Beek, E. M., Wiegant, V. M., Schouten, W. G. P., van Eerdenburg, F. J. C. M., Loijens, L. W. S., van der Plas, C., Benning, M. A., de Vries, H., de Kloet, E. R., & Lucassen, P. J. (2004). Neuronal number, volume, and apoptosis of the left dentate gyrus of chronically stressed pigs correlate negatively with basal saliva cortisol levels. *Hippocampus*, *14*, 688–700. doi:10.1002/hipo.10213

van der Kooij, E. v. E., Kuijpers, A. H., Schrama, J. W., van Eerdenburg, F., Schouten, W. G. P., & Tielen, M. J. M. (2002). Can we predict behaviour in pigs?: Searching for consistency in behaviour over time and across situations. *Applied Animal Behaviour Science*, *75*, 293–305. doi:10.1016/s0168-1591(01)00203-9

Vaughan, E., Le, A., Casey, M., Workman, K. P., & Lacreuse, A. (2019). Baseline cortisol levels and social behavior differ as a function of handedness in marmosets (*Callithrix jacchus*). *American Journal of Primatology*, *81*, e23057. doi:10.1002/ajp.23057

Veissier, I., Boissy, A., Désiré, L., & Greiveldinger, L. (2009). Animals' emotions: Studies in sheep using appraisal theories. *Animal Welfare*, *18*, 347–354.

Versace, E., Morgante, M., Pulina, G., & Vallortigara, G. (2007). Behavioural lateralization in sheep (*Ovis aries*). *Behavioural Brain Research*, *184*, 72–80. doi:10.1016/j.bbr.2007.06.016

Versace, E., & Vallortigara, G. (2015). Forelimb preferences in human beings and other species: Multiple models for testing hypotheses on lateralization. *Frontiers in psychology*, *6*, 233. doi:10.3389/fpsyg.2015.00233

Vetter, S. G., Brandstätter, C., Macheiner, M., Suchentrunk, F., Gerritsmann, H., & Bieber, C. (2016). Shy is sometimes better: Personality and juvenile body mass affect adult reproductive success in wild boars, *Sus scrofa*. *Animal Behaviour*, *115*, 193–205. doi:10.1016/j.anbehav.2016.03.026

Vögeli, S., Lutz, J., Wolf, M., Wechsler, B., & Gygax, L. (2014). Valence of physical stimuli, not housing conditions, affects behaviour and frontal cortical brain activity in sheep. *Behavioural Brain Research*, *267*, 144–155. doi:10.1016/j.bbr.2014.03.036

von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J. N., Marchant-Forde, R., Minero, M., Mohr, E., Prunier, A., Valance, D., & Veissier, I. (2007). Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals - A review. *Physiology & Behavior*, *92*, 293–316. doi:10.1016/j.physbeh.2007.01.007

Wager, T. D., Phan, K. L., Liberzon, I., & Taylor, S. F. (2003). Valence, gender, and lateralization of functional brain anatomy in emotion: A meta-analysis of findings from neuroimaging. *NeuroImage*, *19*, 513–531. doi:10.1016/S1053-8119(03)00078-8

Waller, B. M., & Micheletta, J. (2013). Facial expression in nonhuman animals. *Emotion Review*, *5*, 54–59. doi:10.1177/1754073912451503

Wallez, C., & Vauclair, J. (2012). First evidence of population-level oro-facial asymmetries during the production of distress calls by macaque (*Macaca mulatta*) and baboon (*Papio anubis*) infants. *Behavioural Brain Research*, *234*, 69–75. doi:10.1016/j.bbr.2012.06.004

Wang, C., Burtis, D. B., Ding, M., Mo, J., Williamson, J. B., & Heilman, K. M. (2018). The effects of left and right monocular viewing on hemispheric activation. *Journal of Clinical and Experimental Neuropsychology*, *40*, 198–204. doi:10.1080/13803395.2017.1332169

Watson, S. L., & Ward, J. P. (1996). Temperament and problem solving in the small-eared bushbaby (*Otolemur garnettii*). *Journal of Comparative Psychology*, *110*, 377–385. doi:10.1037/0735-7036.110.4.377

Weary, D. M., & Fraser, D. (1995). Calling by domestic piglets: Reliable signals of need? *Animal Behaviour*, *50*, 1047–1055. doi:10.1016/0003-3472(95)80105-7

Weary, D. M., Lawson, G. L., & Thompson, B. K. (1996). Sows show stronger responses to isolation calls of piglets associated with greater levels of piglet need. *Animal Behaviour*, *52*, 1247–1253. doi:10.1006/anbe.1996.0272

Webb, L. E., Veenhoven, R., Harfeld, J. L., & Jensen, M. B. (2018). What is animal happiness? *Annals of the New York Academy of Sciences*, 1–15. doi:10.1111/nyas.13983

Webster, J. (1994). *Animal welfare : a cool eye towards Eden*. Blackwell Science.

Wechsler, B. (2019). Three levels of consciousness : A pattern in phylogeny and human ontogeny. *International Journal of Comparative Psychology*, *32*, 1–29.

Weiss, A., Adams, M. J., & Johnson, W. (2011). The big none: No evidence for a general factor of personality in chimpanzees, orangutans, or rhesus macaques. *Journal of Research in Personality*, *45*, 393–397. doi:10.1016/j.jrp.2011.04.006

Wells, D. L., Hepper, P. G., Milligan, A. D. S., & Barnard, S. (2017). Cognitive bias and paw preference in the domestic dog (*Canis familiaris*). *Journal of Comparative Psychology*, *131*, 317–325. doi:10.1037/com0000080

Wells, D. L., Hepper, P. G., Milligan, A. D., & Barnard, S. (2018). Stability of motor bias in the domestic dog, *Canis familiaris*. *Behavioural Processes*, *149*, 1–7. doi:10.1016/j.beproc.2018.01.012

Wells, D. L., Hepper, P. G., Milligan, A. D., & Barnard, S. (2019). Lack of association between paw preference and behaviour problems in the domestic dog, *Canis familiaris*. *Applied Animal Behaviour Science*, *210*, 81–87. doi:10.1016/j.applanim.2018.10.008

Wesley, M. J., Fernandez-Carriba, S., Hostetter, A., Pilcher, D., Poss, S., & Hopkins, W. D. (2002). Factor analysis of multiple measures of hand use in captive chimpanzees: An alternative approach to the assessment of handedness in nonhuman primates. *International Journal of Primatology*, *23*, 1155–1168. doi:10.1023/A:1021114518028

Westergaard, G. C., Chavanne, T. J., Lussier, I. D., Suomi, S. J., & Higley, J. D. (2000). Hormonal correlates of hand preference in free-ranging primates. *Neuropsychopharmacology*, *23*, 502–507. doi:10.1016/S0893-133X(00)00141-X

Westergaard, G. C., Lussier, I. D., Suomi, S. J., & Higley, J. D. (2001). Stress correlates of hand preference in rhesus macaques. *Developmental Psychobiology*, *38*, 110–115.

Westergaard, G. C., Chavanne, T., Lussier, I., Houser, L., Cleveland, a., Suomi, S., & Higley, J. (2003). Left-handedness is correlated with CSF monoamine metabolite and plasma cortisol concentrations, and with impaired sociality, in free-ranging adult male rhesus macaques (*Macaca mulatta*). *Laterality: Asymmetries of Body, Brain and Cognition*, *8*, 169–187. doi:10.1080/713754484

Westergaard, G. C., Chavanne, T. J., Houser, L., Cleveland, A., Snoy, P. J., Suomi, S. J., & Higley, J. D. (2004). Biobehavioural correlates of hand preference in free-ranging female primates. *Laterality: Asymmetries of Body, Brain and Cognition*, *9*, 267–285. doi:10 . 1080 / 13576500342000086

Wheeler, R., Davidson, R. J., & Tomarken, A. (1993). Frontal brain asymmetry and emotional reactivity: A biological substrate of affective style. *Psychophysiology*, *30*, 82–89. doi:10.1111/j.1469-8986.1993.tb03207.x

Whiteside, M. A., Bess, M. M., Frasnelli, E., Beardsworth, C. E., Langley, E. J., van Horik, J. O., & Madden, J. R. (2018). Low survival of strongly footed pheasants may explain constraints on lateralization. *Scientific Reports*, *8*, 8–12. doi:10.1038/s41598-018-32066-1

Whitham, W., & Washburn, D. A. (2017). A history of animal personality research. In J. Vonk, A. Weiss, & S. A. Kuczaj (Eds.), *Personality in nonhuman animals* (pp. 3–16). Springer.

Wichman, A., Rogers, L. J., & Freire, R. (2009). Visual lateralization and development of spatial and social spacing behaviour of chicks (*Gallus gallus domesticus*). *Behavioural Processes*, *81*, 14–19. doi:10.1016/j.beproc.2008.12.006

Wildgruber, D., Ackermann, H., Kreifelts, B., & Ethofer, T. (2006). Cerebral processing of linguistic and emotional prosody: fMRI studies. *Progress in Brain Research*, *156*, 249–268. doi:10.1016/S0079-6123(06)56013-3

Winckler, C. (2019). Assessing animal welfare at the farm level: Do we care sufficiently about the individual? *Animal Welfare*, *28*, 77–82. doi:10.7120/09627286.28.1.077

Wittling, W., Block, A., Schweiger, E., & Genzel, S. (1998). Hemisphere asymmetry in sympathetic control of the human myocardium. *Brain and Cognition*, *38*, 17–35. doi:10.1006/brcg.1998.1000

Wolf, M., & McNamara, J. M. (2012). On the evolution of personalities via frequency-dependent selection. *American Naturalist*, *179*, 679–692. doi:10.1086/665656

Wright, J., Bolstad, G. H., Araya-Ajoy, Y. G., & Dingemanse, N. J. (2019). Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. *Biological Reviews*, *94*, 230–247. doi:10.1111/brv.12451

Wright, L., & Hardie, S. M. (2012). Are left-handers really more anxious? *Laterality: Asymmetries of Body, Brain and Cognition*, *17*, 629–642. doi:10.1080/1357650X.2011.615126

Wright, L., & Hardie, S. M. (2015). Left-handers look before they leap : Handedness influences reactivity to novel Tower of Hanoi tasks. *Frontiers in Psychology*, *6*, 58. doi:10.3389/fpsyg.2015.00058

Wright, L., Hardie, S. M., & Wilson, K. (2009). Handedness and behavioural inhibition: Left-handed females show most inhibition as measured by BIS/BAS self-report. *Personality and Individual Differences*, *46*, 20–24. doi:10.1016/j.paid.2008.08.019

Wright, L., Hardie, S., & Rodway, P. (2004). Pause before you respond: Handedness influences response style on the Tower of Hanoi task. *Laterality: Asymmetries of Body, Brain and Cognition*, *9*, 133–147. doi:10.1080/13576500244000265

Wundt, W. (1897). *Outlines of psychology* (Engelmann, Ed.). Leipzig.

Yeates, J. W. (2016). Quality of life and animal behaviour. *Applied Animal Behaviour Science*, *181*, 19–26. doi:10.1016/j.applanim.2016.04.018

Yeates, J. W., & Main, D. C. J. (2008). Assessment of positive welfare : A review. *175*, 293–300. doi:10.1016/j.tvjl.2007.05.009

Zappia, J. V., & Rogers, L. J. (1983). Light experience during development affects asymmetry of forebrain function in chickens. *Developmental Brain Research*, *11*, 93–106.

Zebunke, M., Kreiser, M., Melzer, N., Langbein, J., & Puppe, B. (2018). Better, not just more—Contrast in qualitative aspects of reward facilitates impulse control in pigs. *Frontiers in Psychology*, *9*, 1–12. doi:10.3389/fpsyg.2018.02099

Zebunke, M., Langbein, J., Manteuffel, G., & Puppe, B. (2011). Autonomic reactions indicating positive affect during acoustic reward learning in domestic pigs. *Animal Behaviour*, *81*, 481–489. doi:10.1016/j.anbehav.2010.11.023

Zebunke, M., Nürnberg, G., Melzer, N., & Puppe, B. (2017). The backtest in pigs revisited – inter-situational behaviour and animal classification. *Applied Animal Behaviour Science*, *194*, 7–13. doi:10.1016/j.applanim.2017.05.011

Zebunke, M., Repsilber, D., Nürnberg, G., Wittenburg, D., & Puppe, B. (2015). The backtest in pigs revisited – An analysis of intra-situational behaviour. *Applied Animal Behaviour Science*, *169*, 17–25. doi:10.1016/j.applanim.2015.05.002

Zidar, J., Balogh, A., Favati, A., Jensen, P., Leimar, O., & Løvlie, H. (2017). A comparison of animal personality and coping styles in the red junglefowl. *Animal Behaviour*, *130*, 209–220. doi:10.1016/j.anbehav.2017.06.024

Zonderland, J. J., van Riel, J. W., Bracke, M. B., Kemp, B., den Hartog, L. A., & Spoolder, H. A. (2009). Tail posture predicts tail damage among weaned piglets. *Applied Animal Behaviour Science*, *121*, 165–170. doi:10.1016/j.applanim.2009.09.002

Zucca, P., Cerri, F., Carluccio, A., & Baciadonna, L. (2011a). Space availability influence laterality in donkeys (*Equus asinus*). *Behavioural Processes*, *88*, 63–66. doi:10.1016/j.beproc.2011.06.012

Zucca, P., Baciadonna, L., Masci, S., & Mariscoli, M. (2011b). Illness as a source of variation of laterality in lions (*Panthera leo*). *Laterality: Asymmetries of Body, Brain and Cognition*, *16*, 356–366. doi:10.1080/13576501003690025

Summary

In our Western Cartesian society, it has been a long way to acknowledge animal welfare as a valuable research topic. Nowadays, the five freedoms of farm animals still represent the foundation of animal welfare legislation and ensure animals to fulfil their basic welfare needs. On one hand many efforts have been done to increase their productivity and their physical health which, as a by-product, improved some aspects of their welfare (e.g. absence of malnutrition, less diseases). On the other hand, more research is still needed to address the issues related to their mental health with a recent emphasis on acknowledging farm animals as individuals living a "life worth living". For this reason, animal welfare scientists have the responsibility to improve farm animal lives by conducting research on relevant issues, such as on personality or on positive affective states.

The general introduction (first chapter) aims at laying the conceptual bases and the goals of this thesis. It begins with historical insights into how research on animal welfare emerged and the various ways in which this concept has been defined. I explain why I chose a definition of animal welfare that places the individual and its affective states as a central issue. The topics of personality and emotions are then presented because they may partly explain individual differences in behaviour and physiology, and mechanisms at the origin of affective states respectively. Finally, studying laterality (i.e. asymmetries of brain and behaviour; each brain hemisphere controls the contralateral part of the body) is exposed as a potential approach to gain insights into the common neural mechanisms at the origin of personality and emotions. To illustrate this, several hypotheses on emotional lateralization (i.e. the fact that one hemisphere is specialized for processing specific emotions) are presented and compared. Two of these hypotheses are then selected to study the links of laterality with personality and with emotions. Firstly, the approach-withdrawal hypothesis (the left hemisphere regulates approach behaviours while the right hemisphere regulates avoidance behaviours) is demonstrated as being well-suited to study interactions between laterality and personality. Secondly, the emotional valence hypothesis (the left hemisphere processes positive emotions while the right hemisphere processes negative emotions) is expected to offer an ideal framework to give insight into how emotions are experienced. Some existing applications of laterality research for animal welfare are presented but the need for theory-driven studies in this field is highlighted. This thesis aims at exploring how studying laterality in domestic pigs might provide insight into both their personality and emotions. Thus, it represents the first theory-driven studies on behavioural lateralization in pigs with potential implications for their welfare. The goals of this work are organized according to two main questions: (i) is individual hemispheric dominance (i.e. an individual's "preferred" hemisphere) measurable through individual motor lateralized patterns and does it reflect personality in pigs?

and (ii) can the direct investigation of emotional lateralization in pigs improve understanding of the mechanisms of emotional valence?

The second chapter presents three studies that were published as part of this thesis.

The first study – *Behavioural lateralization in domestic pigs (Sus scrofa): variation between motor functions and individuals* – was published in "*Laterality*" and represents the first study investigating motor lateralization in domestic pigs. We investigated possible motor lateralization patterns in four different motor functions (snout use in a manipulative task, foot use in two stepping tasks, and tail curling) in eighty male piglets. A significant majority of our sample showed individual biases for manipulation with their snout and for curling their tail but not for stepping with their foot. Interestingly, the tail curling was lateralized towards the right at the population level and showed stronger lateralization patterns than snout use. Using a cluster analysis with combined tail and snout laterality, we identified groups of individuals with consistent lateralization patterns across motor functions that potentially reflect the individuals' hemispheric dominance. This new classification system is hypothesized to reflect qualitative differences in brain organization and therefore differences in personality.

As a logical follow-up, investigating how individuals with supposed opposite hemispheric dominance differed in their personality was the aim of the second study – *Assessing animal individuality: links between personality and laterality in pigs*, published in "*Current Zoology*". The approach-withdrawal hypothesis was tested because it may explain differences in boldness or exploration between left and right hemispheric dominant individuals. To analyze the relationships between personality and laterality we tested the same eighty male piglets from the first study in several personality tests and used the classification system integrating two motor functions (tail and snout) that was established in the first study. We found that the combined laterality classification showed both more, and more robust, significant associations with different personality traits compared with the single motor biases. These results supported the approach-withdrawal hypothesis because right-biased pigs (i.e. pigs with a left hemispheric dominance) were bolder and more explorative in a context of novelty than left-biased pigs (i.e. pigs with a right hemispheric dominance). Additionally, right-biased pigs were more sociable (they vocalized more in a context of social isolation) than left-biased pigs. This study demonstrates the importance of taking into account the multidimensionality of both laterality and personality.

The third study – *Visual laterality in pigs: monocular viewing influences emotional reactions in pigs* – was published in "*Animal Behaviour*" and aimed at giving insights into the mechanisms of emotional valence. We used a paradigm of monocular viewing which can be considered as a direct manipulation of the central nervous system, because covering one eye results in a reduced visual input to the contralateral hemisphere. Moreover, the use of emotional conditioning was supposed to allow a focus on emotional valence independently of emotional arousal. Our study tested the emotional valence hypothesis in the context of visual laterality for viewing positive or negative emotionally conditioned stimuli. Ninety male piglets were either positively (food-reward) or negatively (mild punishment) conditioned to an object (a ball). Afterwards, the object was presented without the reinforcer under three different treatments: patch was fixed on the left or right eye (reducing input to the contralateral hemisphere) or patch between the eyes (the control). Monocular viewing had no clear effects on the negatively conditioned subjects. In contrast, in the positively conditioned group, covering the right eye caused a longer interruption of

vocalization, a longer latency to touch the object, a shorter duration of exploring the arena and an increased vagal activity compared to the control. This suggests that reduced processing in the left hemisphere leads to heightened attention that is accompanied by a general orienting response, possibly resulting from a reduced positive appraisal. These findings therefore partially support the emotional valence hypothesis and suggest an important role of the left hemisphere in the quick recognition of a positive stimulus. This study demonstrates that investigating the lateralized processing of emotions can provide insight into the mechanisms of positive appraisal in animals.

The general discussion (third chapter) compiles and summarizes the multiple findings of all three studies. The results of the first and the second studies suggest the existence of individual differences in emotional lateralization that might be at the origin of differences in personality. The third study demonstrates the importance of the left hemisphere for positive appraisal. Considering those studies together shows that studying laterality provides a means to non-invasively elucidate mechanisms underpinning emotional reactions towards a positive stimulus, but also to identify individuals with different cerebral organizations and thus with different personality types. Thus, further investigations of emotional lateralization could be promising to give insight into individual appraisal in pigs. More generally, this thesis demonstrates that studying laterality directly helps to better understand pigs and the novel knowledge generated could already be used to improve their welfare. Indeed, pigs should have the freedom to choose from which side they explore or monitor their environment and more generally how they perceive and react to this environment. Another direct implication is that tail curling might be a complex behaviour that could be impaired if pigs' tails are docked. Further indirect implications for animal welfare are then discussed. Finally, after having suggested some improvements of our studies, potential direct next steps are proposed, such as the investigation of affective styles in farm animals which refer to consistent individual differences in emotional reactivity and regulation.

In conclusion, this thesis supports the idea that using theory-driven studies on emotional lateralization can help advance animal welfare research. More strikingly, it seems that the time has come to investigate affective styles in farm animals. Affective styles may help explain individual differences in appraisal in everyday situations. Understanding those processes could allow us to offer to farm animals living conditions that are in better accordance with what they want and what they like, and thus help heighten their psychological well-being.

Zusammenfassung

In unserer kartesianisch geprägten westlichen Gesellschaft hat es lange gebraucht, um anzuerkennen, dass *animal welfare* (hiernach als Wohlbefinden bezeichnet) ein bedeutsames Forschungsgebiet ist. Heutzutage stellen die sogenannten fünf Freiheiten, mit denen die grundsätzlichen Bedürfnisse von Tieren befriedigt werden, noch immer die Grundlage für Tierschutzgesetze dar. Einerseits wurde viel Mühe investiert, um die Produktivität und die physische Gesundheit von Nutztieren zu verbessern. Daraus resultierten auch einige Verbesserungen verschiedener Aspekte des Wohlbefindens (z.B. keine Mangelernährung, weniger Krankheiten). Andererseits bleibt weitere Forschung notwendig, um die Herausforderungen bezüglich der mentalen Gesundheit von Nutztieren zu bewältigen, da moderne Betrachtungsweisen Nutztiere als Individuen anerkennen, die ein lebenswertes Leben ("*life worth living*") führen können. Aus diesem Grund haben WissenschaftlerInnen, die zum Wohlbefinden der Tiere forschen, die Verantwortung, das Leben von Nutztieren zu verbessern, indem sie adäquate Forschungsfragen untersuchen, wie zum Beispiel Persönlichkeit oder positive affektive Zustände.

Das einführende Kapitel zielt darauf ab, die konzeptuelle Grundlage und die Ziele dieser Dissertation darzustellen. Es beginnt mit historischen Einblicken, wie die Forschung zum Wohlbefinden entstanden ist und wie vielfältig dieser Begriff definiert wurde. Ich erkläre dann, warum ich eine Definition von Wohlbefinden benutze, die sich auf das Individuum und seine affektiven Zuständen fokussiert. Anschließend stelle ich die Themen Persönlichkeit und Emotion vor, weil sie zum Teil individuelle Unterschiede im Verhalten und in der Physiologie bzw. Mechanismen am Ursprung von affektiven Zuständen erklären könnten. Danach zeige ich, dass die Untersuchung von Lateralität (d.h. Asymmetrien von Gehirn und Verhalten, wobei jede Gehirnhälfte den kontralateralen Teil des Körpers kontrolliert) ein potenzieller Ansatz ist, um mehr Erkenntnisse über die gemeinsamen neuronalen Prozesse von Persönlichkeit und Emotion zu gewinnen. Mit diesem Hintergrund werden mehrere Hypothesen zur emotionalen Lateralisation (d.h. die Tatsache, dass eine Gehirnhälfte darauf spezialisiert ist, spezielle Emotionen zu verarbeiten) vorgestellt und verglichen. Ich habe zwei dieser Hypothesen favorisiert, um die Beziehungen von Lateralität mit Persönlichkeit und mit Emotionen zu untersuchen. Einerseits wird die *approach-withdrawal* Hypothese (die linke Gehirnhälfte steuert das Annäherungsverhalten und die rechte Gehirnhälfte steuert das Rückzugsverhalten) als geeignet gesehen, um die Interaktionen zwischen Lateralität und Persönlichkeit zu studieren. Andererseits bietet die Hypothese der emotionalen Valenz (die linke Gehirnhälfte verarbeitet die positiven Emotionen und die rechte Gehirnhälfte verarbeitet die negativen Emotionen) einen idealen Rahmen für mehr Verständnis dessen, wie Emotionen erlebt werden. Dann werden einige beschriebene Anwendungen der Lateralitätsforschung mit Bezug zum Wohlbefinden vorgestellt und der Bedarf an theoriegelei-

teten Studien herausgestellt. Die vorliegende Dissertation soll aufzeigen, wie die Untersuchung der Lateralität beim Hausschwein dazu beitragen kann, Erkenntnisse über deren Persönlichkeit und Emotionen zu gewinnen. Dazu stellt sie die ersten theoriegeleiteten Studien zur Lateralisation von Verhalten beim Hausschwein und potenzielle Konsequenzen für deren Wohlbefinden vor. Die Ziele dieser Arbeit sind durch zwei Hauptfragen spezifiziert. Erstens, ist individuelle Dominanz einer Gehirnhälfte (d.h. die präferierte Gehirnhälfte eines Individuums) durch individuelle motorische Lateralitätsmuster messbar und spiegelt diese Dominanz Persönlichkeit beim Hausschwein wider? Zweitens, kann die direkte Untersuchung von emotionaler Lateralisation beim Hausschwein helfen, die Mechanismen der emotionalen Valenz zu verstehen?

Das zweite Kapitel besteht aus drei Studien, die als separate Teile dieser kumulativen Dissertation veröffentlicht wurden.

Die erste Studie – *Behavioural lateralization in domestic pigs (Sus scrofa): variation between motor functions and individuals* – wurde in der Zeitschrift "*Laterality*" veröffentlicht und stellt die erste Untersuchung zur motorischen Lateralisation beim Hausschwein dar. Wir haben mögliche Muster in der motorischen Lateralisation für vier verschiedene motorische Funktionen (Benutzung des Rüssels beim Manipulieren, Benutzung des Vorderfußes bei zwei unterschiedlichen Lauftätigkeiten und das Drehen des Schwanzes) bei achtzig männlichen Ferkeln untersucht. Eine signifikante Mehrheit unserer Stichprobe zeigte eine individuell lateralisierte Rüsselnutzung und Schwanzdrehrichtung, aber keine lateralisierte Benutzung des Fußes. Interessanterweise zeigte sich eine Verschiebung der Schwanzdrehrichtung hin zur rechten Seite auf Populationsebene, mit stärkeren Lateralitätsmustern als bei der Rüsselnutzung. Mithilfe einer Clusteranalyse wurden die Lateralitätsindizes von Rüssel und Schwanz kombiniert. Dadurch erhielten wir Gruppen von Individuen mit konsistenten Lateralitätsmustern für die beiden motorischen Funktionen. Diese Gruppen könnten möglicherweise Individuen mit hemisphärischer Dominanz darstellen. Es wird vermutet, dass dieses neue Klassifizierungssystem qualitativ verschiedene Gehirnorganisationen und daher Unterschiede in der Persönlichkeit widerspiegelt.

Als logische Folge wurde in der zweiten Studie – *Assessing animal individuality: links between personality and laterality in pigs*, veröffentlicht in der Zeitschrift "*Current Zoology*" – untersucht, wie sich Individuen mit gegensätzlicher hemisphärischer Dominanz in ihrer Persönlichkeit unterscheiden. Die *approach-withdrawal* Hypothese wurde getestet, weil sie Unterschiede in Kühnheit und Erkundung zwischen Individuen mit linker und rechter hemisphärischer Dominanz erklären könnte. Um die Beziehungen zwischen Lateralität und Persönlichkeit zu untersuchen, haben wir die gleichen achtzig männlichen Ferkel aus der ersten Studie in verschiedenen Persönlichkeitstests untersucht. Dazu haben wir die in der ersten Studie etablierte Klassifizierung benutzt, und die zwei motorischen Funktionen (Rüssel und Schwanz) integriert, um Individuen mit potenziell unterschiedlicher hemisphärischer Dominanz zu vergleichen. Wir fanden, dass die kombinierte Lateralitätsklassifizierung mehr und robustere signifikante Assoziationen mit verschiedenen Persönlichkeitszügen zeigte, verglichen mit einzelnen motorischen Präferenzen. Unsere Befunde bestätigten die *approach-withdrawal* Hypothese, weil Tiere mit linker motorischer Gesamtpräferenz (d.h. mit rechter hemisphärischer Dominanz) mehr Kühnheit und Erkundung in einem Neuigkeitskontext zeigten als Tiere mit rechter motorischer Gesamtpräferenz (d.h. mit linker hemisphärischer Dominanz). Zusätzlich waren Tiere mit rechter motorischer Gesamtpräferenz sozialer als Tiere mit linker motorischer Gesamtpräferenz, erkennbar

an einer höheren Vokalisationsrate bei Isolation . Diese Studie weist drauf hin, wie wichtig die Berücksichtigung der Multidimensionalität von Lateralität und Persönlichkeit ist.

Die dritte Studie – *Visual laterality in pigs: monocular viewing influences emotional reactions in pigs* – wurde in der Zeitschrift "*Animal Behaviour*" veröffentlicht und zielte darauf ab, Erkenntnisse über die Mechanismen der emotionalen Valenz zu sammeln. Wir entschieden uns für ein Paradigma des monokularen Sehens, das als direkte Manipulation des zentralen Nervensystems betrachtet werden kann, da, wenn ein Auge abgedeckt wird, auch die Reizwahrnehmung in der kontralateralen Hemisphäre reduziert wird. Außerdem wurde die Hypothese der emotionalen Valenz im Kontext von visueller Lateralität bei Hausschweinen getestet, wenn sie emotional positiv oder negativ konditionierte Reize sehen. Wir haben erwartet, dass die Benutzung emotionaler Konditionierung eine Fokussierung auf emotionale Valenz unabhängig von emotionaler Erregung erlauben würde. Neunzig männliche Ferkel wurden entweder positiv (Futterbelohnung) oder negativ (milde Strafe) konditioniert, während sie ein Objekt (einen Ball) sehen. Nach der Konditionierung wurde das Objekt ohne Verstärker mit drei verschiedenen Behandlungen präsentiert: eine Klappe auf dem linken oder rechten Auge (reduzierter Beitrag der kontralateralen Gehirnhälfte) oder eine Klappe zwischen den Augen (die Kontrollbehandlung). Das monokulare Sehen hatte keine klare Wirkung auf die negativ konditionierten Tiere. Im Gegensatz dazu verursachte das Bedecken des rechten Auges bei den positiv konditionierten Tieren – verglichen mit der Kontrollbehandlung – eine längere Unterbrechung in den Vokalisationen, eine längere Latenz um das Objekt zu berühren, kürzeres Erkunden der Arena und eine erhöhte vagale Aktivität. Diese Befunde lassen vermuten, dass diese Tiere eine erhöhte Aufmerksamkeit kombiniert mit einer generellen Orientierungsreaktion gezeigt haben. Wir haben diese Ergebnisse so interpretiert, dass die reduzierte Verarbeitung in der linken Gehirnhälfte eine weniger positive Bewertung verursacht hat. Diese Befunde unterstützen zum Teil die Hypothese der emotionalen Valenz und suggerieren eine wichtige Rolle der linken Gehirnhälfte in der schnellen Erkennung von positiven Reizen. Die Studie zeigt, dass die Untersuchung von lateralisierten emotionalen Prozessen hilfreich ist, um die Mechanismen von positiven Bewertungen bei Tieren besser zu verstehen.

Das letzte Kapitel fasst die vielfältigen Befunde der drei Studien zusammen. Die Ergebnisse der beiden ersten Studien weisen auf die Existenz individueller Unterschiede in der emotionalen Lateralisation hin, die die Unterschiede in Persönlichkeit erklären könnten. Die dritte Studie zeigt die Beteiligung der linken Gehirnhälfte bei positiven Reizbewertungen. Die gemeinsame Betrachtung dieser Studien zeigt, dass die Untersuchung der Lateralität ein Mittel ist, um Mechanismen nicht-invasiv zu erfassen, die emotionalen Reaktionen auf einen positiven Stimulus zugrunde liegen, aber auch um Individuen mit unterschiedlichen zerebralen Organisationen und somit mit unterschiedlichen Persönlichkeitstypen zu identifizieren. Daher könnten weitere Untersuchungen der emotionalen Lateralisation vielversprechend sein, um mehr Einblicke in die individuelle Bewertung bei Schweinen zu gewinnen. Im Grunde genommen zeigt diese Dissertation, dass die Untersuchung der Lateralität direkt zum besseren Verständnis von Schweinen beiträgt, und dass das neu gewonnene Wissen bereits zur Verbesserung des Wohlbefindens von Schweinen genutzt werden könnte. In der Tat sollten Schweine frei entscheiden, von welcher Seite sie ihre Umwelt erkunden oder beobachten und allgemeiner, wie sie diese Umwelt erfassen und darauf reagieren. Eine weitere Erkenntnis dieser Studien ist, dass das Schwanzdrehen ein

offensichtlich komplexes Verhalten ist, das beeinträchtigt wird, wenn die Schwänze von Schweinen kupiert werden. Weitere indirekte Auswirkungen auf das Wohlbefinden werden diskutiert. Schließlich schlage ich einige Verbesserungen unserer Studien und mögliche nächste Schritte vor, wie z.B. die Untersuchung affektiver Stile bei Nutztieren, d.h. die konsistente individuelle Unterschiede in emotionale Reaktivität und Regulierung.

Zum Schluss unterstützt diese Arbeit die Idee, dass die Verwendung von theoriegeleiteten Hypothesen über emotionale Lateralisation die Forschung zum Wohlbefinden voranbringen kann. Es ist insbesondere an der Zeit, verstärkt auch affektive Stile bei Nutztieren zu untersuchen. Affektive Stile können helfen, individuelle Unterschiede in der Bewertung in Alltagssituationen zu erklären. Das Verständnis dieser Prozesse könnte uns ermöglichen, Lebensbedingungen für Nutztiere anzubieten, die dem entgegenkommen, was sie wollen und was sie mögen, und damit ihr psychologisches Wohlbefinden zu verbessern.

Theses

Objectives of research

Acknowledging farm animals as individuals with their own affective states can promote the willingness to improve their welfare. For this purpose, the frameworks offered by personality and emotion research can be used not only to help improve animal living conditions, but also to raise awareness for farm animals being complex and sentient individuals. Strikingly, the study of laterality (i.e. asymmetries of brain and behaviour; each brain hemisphere controls the contralateral part of the body) is a potential non-invasive approach to gain insights into the common neural mechanisms underpinning both personality and emotions. In this thesis, two main hypotheses about emotional lateralization (i.e. the fact that one hemisphere is specialized for processing specific emotions) are highlighted. First, the approach-withdrawal hypothesis states that the left hemisphere regulates approach behaviours while the right hemisphere regulates avoidance behaviours. Testing this hypothesis through the observation of motor biases is expected as being well-suited to study interactions between laterality and personality. Second, the emotional valence hypothesis states that the left hemisphere processes positive emotions while the right hemisphere processes negative emotions. Testing this hypothesis by analysing the processing of sensory (e.g. visual) information is expected to offer an ideal framework to give insight into how emotions are experienced. This thesis aims at exploring how studying laterality in domestic pigs might provide insight into their personality and their emotions. Thus, this thesis represents the first theory-driven studies on behavioural lateralization in pigs with potential implications for their welfare. The goals of this work are organized according to two main questions that were explored with three studies:

- Is individual hemispheric dominance (i.e. the preference of an individual for using one hemisphere) measurable through individual motor lateralized patterns and does it reflect personality in pigs?
  - Can the observation of individual motor biases be indicative of hemispheric dominance? (Study 1)
  - Are individual differences in motor biases of pigs associated with their personality? (Study 2)
- Can the direct investigation of emotional lateralization in pigs improve understanding of the mechanisms of emotional valence?
  - Does the manipulation of visual information processing (through monocular viewing) in pigs influence their reaction towards stimuli of different valences? (Study 3)

Main findings

The first study – *Behavioural lateralization in domestic pigs (Sus scrofa): variation between motor functions and individuals*, published in *Laterality, Volume 23:5, September 2018, Pages 576-598* – represents the first study investigating motor lateralization patterns in domestic pigs in a multidimensional way.

- A significant majority of piglets showed individual biases for using their snout during a manipulative task and for curling their tail, while a significant majority of piglets did not show any biases for using their left or right foot during stepping.
- Tail curling was lateralized towards the right at the population level and showed stronger lateralization patterns than snout use during a manipulation task.
- Groups of individuals with consistent lateralization patterns across motor functions (tail and snout laterality) were identified with the help of a cluster analysis.

Using the motor biases determined in the first study, the approach-withdrawal hypothesis was tested in the second study – *Assessing animal individuality: links between personality and laterality in pigs*, published in *Current Zoology, Volume 65, Issue 5, October 2019, Pages 541–551*.

- The direction of the single motor biases (for snout use or tail curling) showed significant associations with few personality traits.
- The combined laterality classification (which integrates both functions of snout use *and* tail curling) provideded more, and more robust, significant associations with different personality traits compared with the single motor biases (snout use *or* tail curling).
- The approach-withdrawal hypothesis was supported because right-biased pigs were bolder and more explorative in a context of novelty.
- Right-biased pigs were also more sociable than left-biased pigs because they vocalized more in a context of social isolation.

➔ Using multidimensional approaches to investigate laterality and personality allows us to support the approach-withdrawal hypothesis.

The emotional valence hypothesis was tested in the third study – *Visual laterality in pigs: monocular viewing influences emotional reactions in pigs*, published in *Animal Behaviour, Volume 154, August 2019, Pages 183-192*.

- Monocular viewing, i.e. covering one eye to reduce visual input to the contralateral hemisphere, had no clear effects on the response to a negative stimulus.
- When seeing a positively conditioned object, covering the right eye caused a longer interruption of vocalizations, a longer latency to touch the object, a shorter duration of exploring the arena and an increased vagal activity compared to the control.
- Thus, covering the right eye attenuated the positive appraisal of a positive stimulus.

➔ Monocular viewing tests partially support the emotional valence hypothesis in pigs.

Conclusions

Considering those studies together shows that studying laterality provides a mean for non-invasively elucidating mechanisms involved during emotional reactions towards a positive stimulus, but also to identify individuals with different cerebral organizations and thus with different personality types. Not only do these studies highlight the necessity of offering pigs the freedom to express their side preferences for exploring or monitoring their environment, they might suggest the existence of individual differences in appraisal and possibly of affective styles in pigs.

This thesis supports the idea that using theory-driven studies on emotional lateralization can help advance animal welfare research. More strikingly, it seems that the time has come to investigate affective styles in farm animals. Such affective styles may explain individual differences in appraisal. Understanding those processes could allow us to offer to farm animals living conditions that are in better accordance with what they want and what they like, thus help to heighten their psychological well-being.

"Deine Feinde kennen dich genau
Doch sehen in dir nur dein brennendes Haus
Lachen dich aus und sagen du bist schlecht
Jeden Tag musst du dich beweisen
Ich verbreite deinen Namen auf allen meinen Reisen
Und nie wieder will ich von dir weg

Du bist so ehrlich zu jedem
Du bist so Herrlich dagegen
Ja, du hast mich Groß und stark gemacht
Ich zieh los und such mein Glück
Doch dein Licht zieht mich zu dir zurück"

Mein Rostock (2014) – Marteria

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Now you are reading the best part of this thesis because it will be dedicated to all the people who helped and supported me. (However, be aware that it is the only part which has not been proof-read by Patrick!). I think it will be difficult to express my whole gratitude in English which is not my mother tongue. At least I am used to this issue in German after more than 5 years in Mecklenburg-Vorpommern...

Before acknowledging the people, I want to thank all **the pigs** who participated in my experiments. This thesis has been written during the (Chinese) year of the Pig and I hope it will honour you. Sometimes I still feel ashamed about the prejudices I had on your species. I enjoyed so much working with you: you looked so joyful, and you surprised me almost everyday. Also, you looked so human when you were satisfyingly chewing the chocolate raisins! Each time I had to begin a new replicate (and therefore I had to say goodbye to you) was a very heartbreaking moment. I hope I communicate enough my fascination for you so that people in my own circle develop more empathy for you...

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[1] Franks, B., Chen, C., Manley, K., Higgins, E. T. (2016). Effective challenge regulation coincides with promotion focus-related success and emotional well-being. *Journal of Happiness Studies, 17*, 981–994 . doi:10.1007/s10902-015-9627-7

[2] www.sciencewithstyle.org/blog/category/black-belt-phd

Lisette, "A PhD is hard. But a good supervisor makes it much easier."[3] Like the author of these words, I am very grateful for having had you as a supervisor. I remember how afraid I was when you had your first maternal leave... but you were so committed that you still remotely supervised me. Thank you for that in particular. Of course it was not always easy, but even in the hardest times you supported me: either with a little joke (e.g. "When things don't go right, go left!") or with meaningful words (e.g. "Always remember that we both want to give our best"). After our long (scientific) discussions, I always felt cognitively enriched and enthusiastic that you valued my ideas and opinions (i.e. this famous state of positive arousal). Through your guidance and your patience, I learned how to write and structure good papers, something I thought (some years ago) I never would be able to do. Finally, (and maybe most importantly) your feedback and criticism made me grow scientifically during the writing process (in particular of this thesis), and thanks to this, I think I have now a better idea about the trade-offs between self-criticism and self-confidence. Also, thank you for having made me discover that laterality is a much wider and cooler research field than I thought!

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[3] White, E. M. (2018). The best supervisor *Nature Careers, 562*, 297.

On the road to Wokrent, I saw a weird cloud, and later I heard that it was a tornado[4]! Besides being a very funny person, you are a reliable colleague who not only helped me in the experiments (and checked the references of this thesis!) but who also could advise me on any question about the ANS. Your help was very precious. I find our discussions about science, family and career always very insightful. In the last months you supported me a lot, I would like to thank you for your open ear. Also, partly because of you, my acknowledgements are very long. Indeed, I hope I am citing you correctly: "You should even be thankful for any friend who had a drink with you in the last months, because they inspired you". Unfortunately, I probably forgot some people...!

Antonine, thanks to you, I was not the only French person at the institute! Moreover, your expertise in animal personality helped me a lot. I really enjoyed our scientific adventures together: the funny excursion to the PhD Seminar in Potsdam and the preparation for the *Lange Nacht der Wissenschaften* will remain very nice memories. It was also great to discover our common interest outside work in contributing for a little European organization: I will always remember the great performance you did for the European Balcony Project. Besides all this, it was always a pleasure to go to the Kantine together and to support each other.

Borbala, your ideas and opinions were always very refreshing. I am happy that we could manage (with Antonine and Annika together) to create our little Kantine-"personality workshop". Now you are far away but I still hope that we could collaborate in the future!

Jenny, I met you for the first time in the EAS (on the day of my interview) and I was already struck by your energy, kindness and openness. I really enjoyed your company in the office... but I know, at the beginning, I may have been a straining colleague who were all the time asking stupid questions! You also helped me a lot in the EAS when I had to get familiar with the technique. Also, you gave me the possibility to live in Wokrent when you left the institute. All in all, you improved my well-being until your last minute at the FBN, thank you for that!

Susen and **Roberto**, or should I say sunny girl and sunny boy? ;) Thank you for your constant good mood, which was (sometimes) contagious. In our little office/kitchen, you reminded me very often how important it is to focus on a healthy work-life balance. Thank you, Susen, for our detailed discussion about the 5 freedoms, I could make last minute corrections in this thesis!

Thanks to the other PhD-students of our group for being so nice: **Volker**, **Maren K.** and **Neele**.

I am also grateful for all the people who spent hours analyzing our videos: **Maren K.**, **Regina**, **Kathrin Kempchen** and **Linda Nuding**.

Petra and **Ellen**, thank you for your precious help in the analysis of cortisol and testosterone.

Manu and **Jan**, I also have to thank you for insightful advice when I needed to know something about the backtest or conditioning. Hearing your opinions was very enriching!

Christian N., thank you for your enthusiasm and for having instaured the Journal Club as a regular meeting. Also, you motivated me to have a Twitter account which was a big step for me!

Jutta, you are the sunshine of our corridor and because you are so kind, the first words we exchanged were in French. Thank you for your help when I had to write complicated forms such as *Dienstreiseanträge* or when I needed an additional *Hefter*, or *Ordner*, or *Klammer*... the list is long, and there are still so many other material for which I don't the name neither in German nor in French!

[4] www.spiegel.de/panorama/gesellschaft/tornado-in-buetzow-buergermeister-grueschow-ueber-das-unwetter-a-1032388.html

Kurt and **Peter**, I thank you for your social support, especially during the time I felt really lonely. You offered me some coffee, and we talked about Adobe Audition, music, culture and radio. Besides helping me for creating a conditioning tone for the pigs, it inspired me for the radio shows later!

Finally, I want to thank all the other colleagues of the Insitute of Behavioural Physiology who contribute to pleasant everyday working conditions!

There are two FBN-friends/colleagues from other institutes I would like to thank: **Zahra**, it was a chance to learn to know you just before you left! I hope I can visit you soon; **Lidia**, thank you for being the best cat-sitter ever but also for having convinced me to do more sport! You are a very inspiring person.

Patrick, thank you so much again for having proof-read my whole thesis. It has been an honour for me that you have accepted this task!

A very special thank goes to **Frau Lindenbeck** from *Arbeitsamt* who was very understanding, sympathetic and supportive during the last months. It definitely helped me to work on my thesis as focused as I could.

Two additional women whom I consider to be colleagues (because they are also PhD students) but also best friends for this tough time: Alice and Kristina.

Alice, first, thank you for having taken the time to give me your feedback for this thesis. I think you are right, I actually should spend some additional months just for writing these never ending acknowledgements. However, in our case, I think that writing a book only about our friendship would be more appropriate. It wouldn't be the first and last project that we plan together (e.g. the 13th warrior movie project)... We almost know each other since 10 years and I never would have thought that you would become so important in my life! I hope I can support you as much as you support me. Knowing that I have you makes me reach such a high level of mental well-being. Beyond our similar academic background, it is amazing to see how often we feel the same, have the same fears (except for the **** forest), the same existential questioning. I wish we both will reach what we want from life, and can continue our never ending discussions *for ever*.

Kristina, thank you for the first paragraph of my Preface that you peer-reviewed. You and me arrived in Rostock quite simultaneously and for the same reason. We both discovered the city sometimes together, with or without *Sperrmüll*. I felt so happy and understood when I noticed you love to discuss about etymology, you are such an Encyclopedia! Almost like a mentalist with superpowers, when I do mistakes in German, you correct me and directly explain me why I did this mistake in particular. Since we agreed on the theory about *Schrebergarten*, you definitely contributed to my successful integration in Germany. Indeed, we own a *Schrebergarten*, therefore we are (i) an old couple and (ii) very German. Maybe we still struggle with one last thing in this region: the wind and the winter. When it's cold, we tried not to be "*Exilée intérieur / Accrochée a son radiateur*[5]" Thank you for all the (emotional) support you gave me when I needed it. You are such a great person and I am so happy to be a friend of yours.

Julien, you are also almost a colleague now! Thank you for having given me your feedback on a previous version of this thesis. And thank you for having played the game of "puppet master in Germany", I hope you are not traumatized though! Also thank you for having complimented our *Schrebergarten* with your naturalist's point of view!

[5] L'hiver indien (2017) – Baloji

A special thank to all the friends who lived with me, and therefore supported me in any way: **Charlie**, for being my little Rostocker brunette fairy and thus for integrating me in this city and in the "Gabi-Kollektiv", it changed my life. I think I officially used your *Gutschein um sich in Rostock zu verlieben*! **Nicole** and **Antoine**, for making the Wokrent dream and the Wokrentival true.

For a French person, it is not always easy to live in Northern Germany, therefore I would like to thank all my friends and family who came from far away, just for visiting me: **Melanie** and **Lucie** (from French Guiana: a true proof of love!), I still feel very guilty for not having taken the time yet to visit you. **Corinna**, my little Viennese brunette fairy. **Fanny**, my little French brunette fairy, who even used her superpowers in Rostock and made me meet **Binka**, and through Binka, I could meet **Maria**. A literal hippie chain reaction! **Marie and François**, **Cilli**, **Christine and Vincent**, **Catherine and Jean-Marc**, **Viviane and Björn**, **Pierre and Rebecca** (but you both are cheaters, you stopped in Hamburg! :p), **Nicolas and Clémence**, **my parents**, **Pierre and Christina**, **Georg**, and **Isaline**. I hope you also liked the Baltic sea and enjoyed discovering the place where I live :)

Some special friends who don't belong to any category previously mentioned but who also changed my life: **Lisa**, for having opened your heart to me from the beginning. You are a very stimulating person. I love our discussions and listening your point of views is a very refreshing activity to me. Thanks to you: I am in our Gospel choir, I was at a Marteria concert,... **Frida**, I really enjoyed the phase when we went every week swim together. Most importantly, our exciting discussions about mental well-being helped me a lot, and I think you know for what I am the most grateful...;)

I want to write a big up for all the wonderful babies I know who were born during my thesis (note that the sex ratio is 50 – 50!): **Philéas and Valentin**, **Stefano and Danilo**, **Jonas**, **Justus**, **Milan**, **Jelsa**, **Sophie**, **Louisa**, **Timothée**, **Julia**, **Alida and Anna Elfie**, **Olivia and Nathalie**, and so many future babies!

Eva-Maria, thank you for caring so much about my career. Your advice is golden.

Finally, I want to thank my whole beloved family: **my parents**, my sister: **Catherine** and my brothers: **Pierre and Nicolas**. You all know that without you, I wouldn't be the person I am now, and I wouldn't have achieved this big challenge. For more details, I invite you to read again the acknowledgements of my Vet-thesis, because nothing changed concerning my gratitude ;). I also have a special thought for my godmother **Gudrun** who supported me a lot but who passed away last year.

The last (but not least) "human" thank goes to **Helmut**. I think you are the person I have to thank the most. Especially for this last year during which I showed my dark side: I was very stressed, exhausted and very often in a bad mood. Thank you for having been present **everyday** and for having supported me always when I needed (in both terms, English and French: *Merci de m'avoir supportée*). You helped me exactly enough so that I could help myself, this is inestimable. Besides this, you are one of the most inspiring persons I know: so much potential of creativity for both science and art. It is so exciting to continue our adventure together. Since you like efficient communication, I will just conclude with a nice sentence: "Loving you has made my life so beautiful"[6]

Big thanks to my wonderful two cats **Wasi** and **Frisi** who intensively encouraged me during this whole marathon and who made me feel not alone when I was writing at home.

[6] Loving you (1974) – Minnie Riperton

This thesis is dedicated to Flippon (May 2004 – June 2018)

Scientific Curriculum Vitae

Charlotte Goursot, graduated from the National Alfort Veterinary School (DVM) and from the University of Strasbourg (M.Sc.)

Education

2014-2019	PhD Student at the Leibniz Institute for Farm Animal Biology, Institute of Behavioural Physiology, FBN Dummerstorf
2014	Doctor in Veterinary Medicine (DVM), University Paris 12
2012-2013	Master (M.Sc.) in Ecophysiology & Ethology, University of Strasbourg
2008-2013	Veterinary Study Diploma, National Alfort Veterinary School • *Including three theoretical years, one semester in the Universitary Veterinarian Hospital Center of Alfort, one semester of rural practice, and one year of research specialization. Level 1 diploma of the Wild Life Center*
2006-2008	Preparatory studies for highly selective nationwide entrance examinations for the French "Grandes Ecoles", St. Louis High School, Paris • *Biology, Chemistry, Physics & Earth Sciences*
2006	European Baccalaureate with German mention, Charles Péguy High School, Orléans • *Scientific specialization*

Grants & Awards

ENVA, 2015	Veterinarian thesis price (silver medal) for the Doctorate in Veterinary Medecine in Maisons-Alfort, France • *13th November 2015*
CogEvo, 2019	Abstract award for the 6th Workshop on Cognition and Evolution in Rovereto, Italy • *10th-13th July 2019*
DAAD, 2019	Congress grant for the 53rd Congress of the International Society for Applied Ethology (ISAE) in Bergen, Norway • *5th-9th August 2019*

Internships

2014	CNRS of Rousset, Primate Station (UPS 846) • *Fecal cortisol assay in 4 captive rhesus macaques (Macaca mulatta)* • Supervised by Pau Molina Vila and Romain Lacoste (two months)
2013	DEPE of Strasbourg (CNRS IPHC, UMR 7178) in collaboration with the Department of Cognitive Biology & Messerli Research Institute (Vienna) • *Testing the biological market theory with a cooperative string pulling task by keas (Nestor notabilis)* • Haidlhof Research Station, Austria • Supervised by Ronald Noë, Gyula Gajdon and Thomas Bugnyar (eight months)
2012	Comparative Ethology & Cognition Laboratory (LECC), Nanterre, France • *Study of neophobia by canaries (Serinus canaria) and helping with blood sampling* • Supervised by Eric Vallet (one month)
	Rural veterinary clinic at Le Vigan (southern France) and Sellières (eastern France) • Assistant of rural veterinarians in their daily activities (two months)
2011	LPO (French non-governmental organisation for wild birds) of l'île Grande, (north-western France) • *Volunteer assistant for birds health care, museum and touristic guide* (one month)
	Leibniz Institute for Zoo and Wildlife Research, Department of Reproduction Management, IZW Berlin • *Role of Syncytin in embryonic resorption by mice (Mus Musculus)* • Supervised by Barbara Drews (one month)
2010	Leibniz Institute for Zoo and Wildlife Research, Department of Reproduction Management, IZW Berlin • *Study of embryonic resorption by hares (Lepus europaeus) (Ultrasound imaging, DNA extraction, histology), analyzing ultrasound images of giraffe's embryos* • Supervised by Barbara Drews (two months)
2009-2010	Veterinary Medicine at Freie Universität of Berlin • Erasmus exchange program (two semesters)
2008-2009	Rural veterinary clinic at Frasne (eastern France) • *Following a rural veterinarian for daily activities* (one week)
	Dairy cattle management at Bief-du-Fourg (eastern France) • *Zootechnical survey including behavioural observations & analysis of the reproduction management over a one-year period of a dairy cattle herd* (one month)

Courses attended

09/07/2015	Scientific writing, FBN Dummerstorf • *3 hours in English*
07-09/09/15	Introduction to SAS, TI Braunschweig. Structure of SAS, data input and evaluation, frequency distribution, statistics analysis, data visualization • *15 hours in German*
2018	Learning R, FBN Dummerstorf.Atomic and non-atomic vectors, conditions, simple and advanced loops, functions, R-Packages • *30 hours in English*
2018	Statistics course, FBN Dummerstorf. Introduction to statistics, estimation and comparison of parameters, analysis of variance, correlation and regression • *40 hours in English*
11-12/11/19	Graduate Academy, University of Rostock: Grant proposal writing - How to design and communicate your project convincingly • *14 hours in English*
02-06/03/20	Dahlem Research School, Freie Universität Berlin: Introductory course to statistics. Solving problems in biostatistical analysis and experimental design in the life sciences • *35 hours in English*

Science popularization

2016-2019	"Science caravan", FBN Dummerstorf – Laterality, interactions with emotions and personality • Animation and workshop organization for German pupils • *90 minutes in German*
26/04/18	"Long night of sciences", University of Rostock – "Why can behaviour help improving animal welfare?" • *Animation in German of the FBN stand, in cooperation with Marie-Antonine Finkemeier & Norbert Borowy*

Languages	**Softwares**
French: mother tongue	Statistics (R, SAS, JMP), Behaviour (The Observer, Solomon),
English: fluent	Bioacoustics (Avisoft), Heart rate variability (Polar Precision
German: fluent	Performance), Geographic information systems (ArcView),
Italian: basics	Graphical software (SigmaPlot, Photoshop), LateX

Science communication

24-25/09/15	3rd Leibniz PhD Symposium : "Keep it simple!-Science Communication", Berlin (DE) – Functional lateralization in domestic pigs (Sus scrofa): interactions with emotions and personality • *Poster in English*
04/11/15	PhD-day of Leibniz Institute for Farm Animal Biology, FBN Dummerstorf (DE) – Functional lateralization in domestic pigs (Sus scrofa): interactions with emotions and personality • *Beginners section / Talk - 5 minutes in English*
19-21/11/15	47th International Society for Applied Ethology of West Central Europe and Deutsche Veterinärmedizinische Gesellschaft, Freiburg (Breisgau, DE) – Functional lateralization in domestic pigs (Sus scrofa): interactions with emotions and personality • *"Promovierende stellen sich vor"/ Talk – 3 minutes in English*
03-05/06/16	Graduate Meeting in Animal Behaviour, German Zoological Society, Biological Station Gülpe (DE) – Functional lateralization in domestic pigs (Sus scrofa): interactions with emotions and personality • *Talk – 15 minutes in English*
12-15/07/16	8th European Conference of Behavioural Biology, Vienna (AT) – Investigating motor lateralization patterns in domestic pigs (Sus scrofa) • *Poster in English*
17-19/11/16	48th International Society for Applied Ethology of West Central Europe and Deutsche Veterinärmedizinische Gesellschaft, Freiburg (Breisgau, DE) – Untersuchung der motorischen Lateralität beim Hausschwein (Sus scrofa) • *Poster in German*
13/12/16	Guest Seminar, University of Potsdam (DE) – Functional lateralization in domestic pigs (Sus scrofa): interactions with emotions and personality • *Talk – 20 minutes in English*
11/11/17	PhD-day of Leibniz Institute for Farm Animal Biology, FBN Dummerstorf (DE) – Interactions between laterality and personality in the domestic pig (Sus scrofa) • *Advanced section / Talk - 15 minutes in English*
22-24/11/18	50th International Society for Applied Ethology of West Central Europe and Deutsche Veterinärmedizinische Gesellschaft, Freiburg (Breisgau, DE) – Visuelle Lateralisation und affektive Reaktionen beim Hausschwein • *Talk – 15 minutes in German*
01/04/19	Colloquium, FBN Dummerstorf (DE) – Functional laterality in pigs: interactions with personality and emotions • *Talk – 45 minutes in English*
10-12/07/19	6th Workshop on Cognition and Evolution (CogEvo2019), Rovereto (IT) – Functional lateralization in pigs: Interactions with emotions and personality • *Poster in English*
05-09/08/19	53rd Congress of the International Society for Applied Ethology (ISAE), Bergen (NO) – Visual laterality in pigs and the emotional valence hypothesis • *Talk – 15 minutes in English*
18/09/19	Guest Lecture, Vetmeduni of Vienna (AT) – Functional laterality in pigs: interactions with personality and emotions • *Talk – 45 minutes in English*

List of Publications

Peer-reviewed journal articles

C. Goursot, S. Düpjan, A. Tuchscherer, B. Puppe & L. M. C. Leliveld (2018). Behavioural lateralization in domestic pigs (*Sus scrofa*) - Variations between motor functions and individuals, Laterality: Asymmetries of Body, Brain and Cognition, Volume 23:5, September 2018, Pages 576-598 10.1080/1357650X.2017.1410555

C. Goursot, S. Düpjan, E. Kanitz, A. Tuchscherer, B. Puppe & L. M. C. Leliveld (2019). Assessing animal individuality: Links between personality and laterality in pigs, Current Zoology, Volume 65, Issue 5, October 2019, Pages 541–551 10.1093/cz/zoy071

C. Goursot, S. Düpjan, A. Tuchscherer, B. Puppe & L. M. C. Leliveld (2019). Visual laterality in pigs: Monocular viewing influences emotional reactions in pigs, Animal Behaviour, Volume 154, August 2019, Pages 183-192 10.1016/j.anbehav.2019.06.021

Dissertations

C. Goursot, (2014). Théorie du marché biologique: étude préliminaire chez les Kéas (*Nestor notabiblis*) • *Monography for the DVM (Doctor of Veterinary Medicine) degree. Defended on the 31st January 2014*

C. Goursot, (2020). Laterality in pigs and its link with personality, emotions and animal welfare • *Cumulative dissertation for the Dr.agr. (PhD) degree. Defended on the 15th September 2020*

Conference Proceedings

C. Goursot, S. Düpjan, C. Kalbe, E. Kanitz, B. Puppe, A. Tuchscherer & L. M. C. Leliveld (2016). Untersuchung der motorischen Lateralität beim Hausschwein (*Sus scrofa*). KTBL- Schrift, 511: 273-275

C. Goursot, S. Düpjan, A. Tuchscherer, B. Puppe & L. M. C. Leliveld (2018). Visuelle Lateralisation und affektive Reaktionen beim Hausschwein. KTBL-Schrift, 514: 24-34

C. Goursot, S. Düpjan, A. Tuchscherer, B. Puppe & L. M. C. Leliveld (2019). Visual laterality in pigs and the emotional valence hypothesis, ISAE Bergen-Norway. Wageningen Academic Publishers, 133